FIGURE 1. Stratigraphic occurrence of zosterophyll, pre-lycopsid, and lycopsid genera in Silurian–Devonian strata.

Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
Zosterophylls and Lycopsids

453

FIGURE 2.   Line drawings of plants with zosterophyll-like sporangia. Sporangia are stippled.—A. *Hicklingia edwardii*—assigned to the zosterophylls by Edwards (1976). B–D. Probable rhyniophytes.—B. *Huia recurvata* Geng, 1985.—C. *Hsüa robusta* Li, 1982.—D. *Renalia hueberi* Gensel, 1976. E, F. Incertae sedis.—E. *Nothia aphylla* El-Saadawy & Lacey, 1979.—F. *Eophyllophyton bellum* Hao, 1988.

Even though the earliest undoubted lycopsid, *Leclercqia*, is found in Emsian and Givetian strata, uncertainty about the time of appearance of ly-copsids remains. If *Baragwanathia* is a lycopsid, and if the Ludlow age of some Australian *Baragwa-nathia* is correct, lycopsids would have existed in the mid–late Silurian. As yet undescribed zoster-ophylls are reported from comparable age sedi-ments in Australia (Tims & Chambers, 1984), and thus the two groups may have co-occurred in the late Silurian.

In light of these developments, and despite the constraints of imperfect representation in the fossil record, it is appropriate to evaluate the position of zosterophylls relative to lycopsids once again. Spe-cifically, how do zosterophylls relate to the lycop-sids—do they represent a paraphyletic group with respect to the lycopsids (i.e., are they ancestral?), or might they be a monophyletic sister group, or do they have only a distant relationship to lycop-sids? This paper will consider these questions by (1) characterizing zosterophylls, putatively related taxa, and selected lycopsids in terms of their struc-tural organization, growth habit, reproduction, and ecology, and (2) considering prevailing theories concerning how lycopsids may have arisen. This is

followed by an analysis of relationships of zoster-ophylls, pre-lycopsids, and lycopsids within the con-text of major pteridophyte lineages using cladistic methods of phylogenetic reconstruction. Some spe-cific questions to be dealt with in the course of this evaluation are the following: (1) Is the morphology of these plants complex enough to allow such a question to be answered definitively? (2) Do the patterns of diversity and directions of morpholog-ical change differ significantly between these two groups? (3) Do ecological patterns of zosterophylls differ from those of early lycopsids? (4) Do the differences in their morphologies and ecologies con-strain them into different evolutionary directions?

GENERAL FEATURES OF ZOSTEROPHYLLS

If one surveys the array of plants assigned with some assurance to zosterophylls, the following are characteristics common to the majority of them: plants with a rhizomatous habit, in which axes bifurcate isotomously and/or anisotomously (Fig. 3A, C, D) at frequent to infrequent intervals. Some exhibit H or K branching, in either prostrate and aerial, or only aerial, portions of the plant. H and K branching has been variously interpreted in the
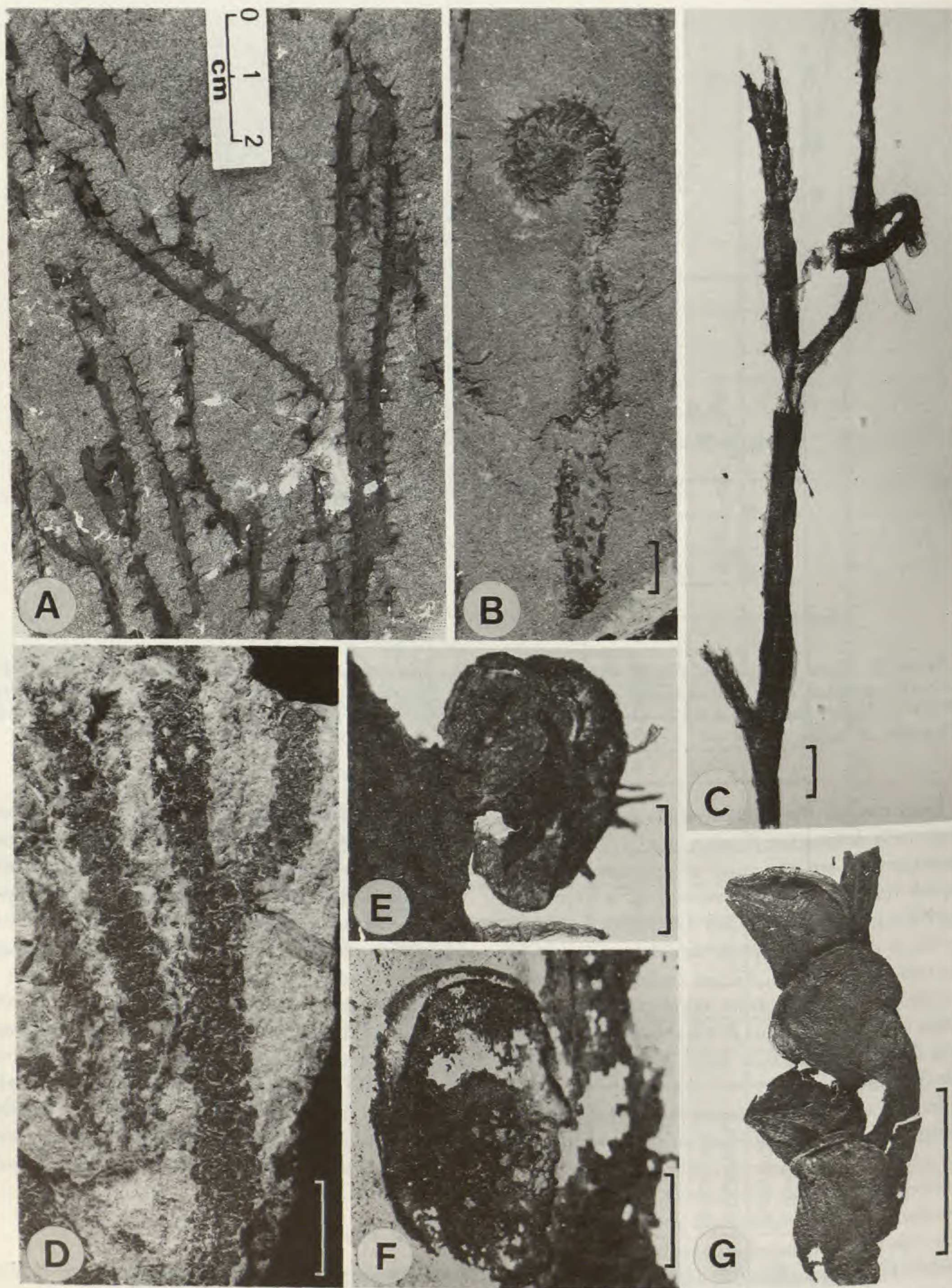
FIGURE 3. A. Several axes of *Sawdonia ornata* from Gaspé, Canada. Central one bears sporangia.—B. Circinate axis of *Sawdonia ornata* from New Brunswick, Canada.—C. Branched axis of *Crenaticaulis verruculosus*, with subaxillary branch at upper right.—D. Sparsely branched new zosterophyll from New Brunswick covered with globose emergences.—E. Sporangium of *Sawdonia ornata* from Gaspé showing short stalk, two valves and emergences on outer valve.—F. Sporangium of *Oricilla bilinearis* from New Brunswick illustrating short stalk, horizontal orientation relative to axis.—G. Several sporangia of *Zosterophyllum divaricatum* from New Brunswick, illustrating upright orientation. Note the thickened area adjacent to dehiscence region. F from Gensel (1982b). G from Gensel (1982a). B–D, G scale bars = 5 mm. E, F scale bars = 1 mm.

Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
Zosterophylls and Lycopsids

455

literature; I view it as a result of flattening during fossilization of branched axes of a plant consisting of a prostrate, dichotomizing rhizome from which upright branches depart. Certain types of dichotomy in upright axes also could produce this pattern when flattened, as demonstrated by Gerrienne (1988) and Edwards & Kenrick (1986).

Several taxa exhibit subaxillary tubercles, branches (Fig. 3C), or scattered protuberances ranging from small stubs to branched axes (discussed in detail by Edwards & Kenrick, 1986). These suggest some instability in developmental patterns of shoot apices. Circinate vernation of axes (Fig. 3B) is known for several genera.

Axes are either smooth or covered with emergences that vary in morphology and arrangement depending on the taxon (Figs. 5, 6). A few taxa exhibit emergences on sporangia (*Sawdonia*—Fig. 3E, *Discalis*, *Koniora*, and a new taxon from New Brunswick).

Where known, anatomy consists of an exarch, round to elliptical haplostele (Fig. 7A, C). Protoxylem, recognized mainly on the basis of smaller cell diameter, consists either of a single layer or of several clusters of a few small tracheids located around the periphery of the xylem strand. The outline of the stele is smooth in contrast to the ridged or lobed appearance of steles in early lycopsids. Tracheid wall pattern according to Kenrick & Edwards (1988a) is annular, helical, indirectly connected annular or helical, and possibly scalariform to bordered pitted (*Koniora*). Kenrick & Edwards (1988a) also demonstrated the presence of irregular perforations on walls in between the annular thickenings (not considered an artifact of preservation) in *Gosslingia*, *Thrinkophyton*, and *Deheubarthia* and noted that some other zosterophylls, pre-lycopsids, and early lycopsids may show a similar condition (Fig. 10B). Figure 7B confirms the same pattern for *Crenaticaulis*. The outer cortex in several taxa consists of thickened cells just below the epidermis (Fig. 7A).

Cuticular features are known to different extents among the zosterophylls. Epidermal cell shape varies from elongate-rectangular to nearly isodiametric in *Zosterophyllum* (Lele & Walton, 1961) and in some other genera. Several genera in which cuticles have been studied exhibit the distinctive "rosette cell" pattern (Fig. 7D, E) first noted in *Sawdonia ornata* by W. N. Edwards (1924). Papillae occur on epidermal cells in *Sawdonia* (Fig. 8B) and *Crenaticaulis*. Both of these features are absent in *Zosterophyllum*, however. Stomata are interpreted as consisting of two guard cells surrounded by epidermal cells (Figs. 7F, 8A), even
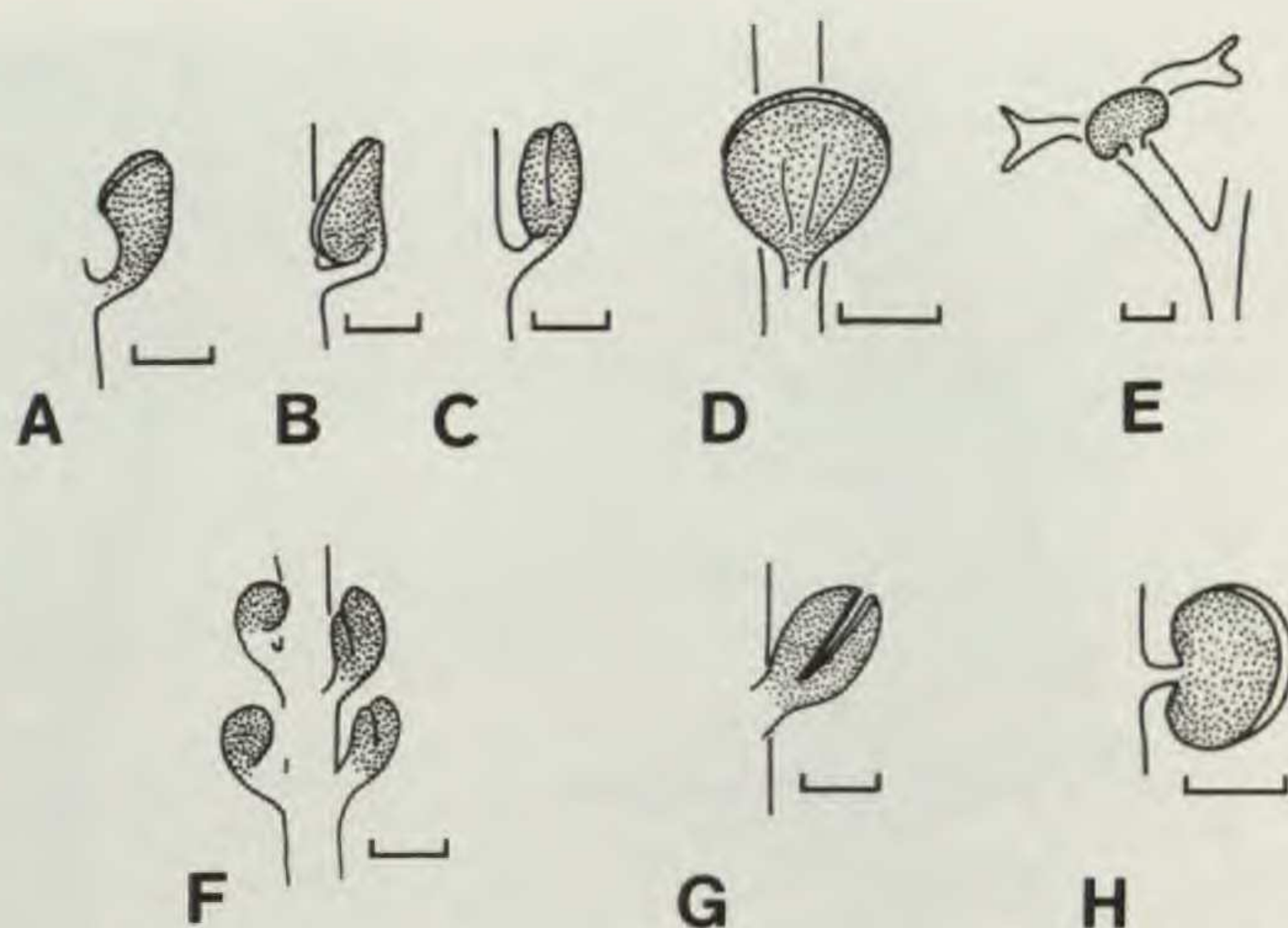

FIGURE 4. Sporangial orientation in zosterophylls. A–G. Upright orientation.—A–D. *Zosterophyllum*.—E. *Koniora*.—F. *Crenaticaulis*.—G. *Sawdonia*.—H. Horizontal orientation. *Oricilla*. Also present in *Tarella*, *Gosslingia*, perhaps *Anisophyton* and *Margophyton*. Scale bars = 2 mm.

though the cuticular impressions do not delimit two guard cells. The basis for this interpretation is the presence of T-shaped thickenings at the stomatal poles, and the occasional presence of a faint dividing line that would delimit guard cells in the cuticle of *Zosterophyllum myretonianum* (Lele & Walton, 1961; Edwards et al., 1982). In some taxa stomata appear sunken.

Sporangia are borne laterally on axes and terminate stalks ranging from less than 1 mm to 4 mm long. Sporangial stalks in *Zosterophyllum* are reported to be vascularized. Sporangia are reniform or occasionally globose in outline and dehisce along their distal margins (transverse dehiscence) into equal or unequal valves. In several taxa, compression remains of sporangia exhibit a thickened border adjacent to the dehiscence line (an annulus?). Anatomy of *Zosterophyllum llanoveranum* sporangia (Edwards, 1969) shows the thickened margins to consist of up to nine layers of elongate, thick-walled cells; in between these borders are some thin-walled cells, some of which probably broke down to cause sporangium opening.

Sporangia are oriented with respect to the axes in one of two ways: (1) upright—their stalks are parallel or at an acute angle to the axis such that their dehiscence lines are perpendicular to the axis bearing them (Figs. 3E, G, 4A–G); or (2) horizontal—their stalks are perpendicular to the axes so that their dehiscence line parallels the axis (Figs. 3F, 4H). Spores are trilete, smooth or slightly granular, sometimes with curvaturae perfectae. They are very similar throughout the group (Fig. 8C, D). *Zosterophyllum myretonianum*, *Z. divaricatum*, *Gosslingia*, *Sawdonia*, *Crenaticaulis*, *Thrinkophyton*, and *Deheubarthia* are among the
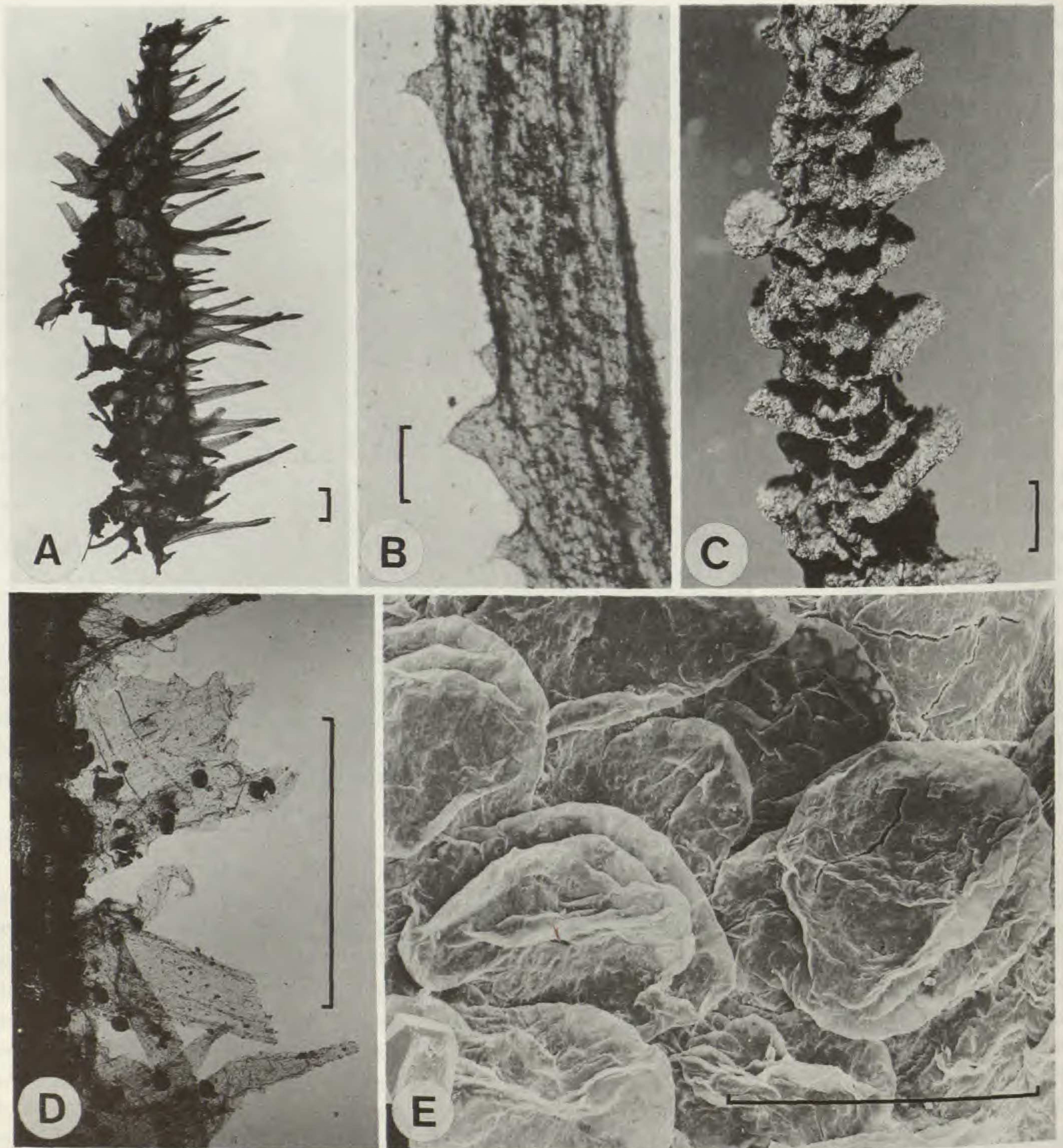
FIGURE 5. Emergence types in zosterophylls.—A. Tapered spinelike emergences of *Sawdonia ornata.*—B. Papillae and short deltoid emergences (teeth) in opposite rows on axis of *Crenaticaulis verruculosus.*—C. New zosterophyll type b from New Brunswick with flattened wedgelike emergences.—D. Forked and entire spinelike emergences of *Sawdonia acanthotheca* from New Brunswick. One near the top has eight tips.—E. Scanning electron micrograph of globose emergences in a new zosterophyll type from New Brunswick; general view is in Figure 4D. Scale bars = 1 mm.

more completely known zosterophylls: they exhibit several branching orders, at least some aspects of anatomy, and bear sporangia.

Zosterophylls vary greatly while retaining a basic sporangium morphology and attachment that unite the group. An assessment of the characters useful in recognizing genera is presented by Kenrick & Edwards (1988b) and Edwards et al. (1989). The former note that each new taxon presents a new "concatenation of overlapping characters" with the others. The characters they regard as useful

are: (1) sporangium distribution on axes; (2) sporangium arrangement (spiralled, linear, variable, singly); (3) sporangium orientation, e.g., sporangium upright or horizontal; (4) sporangial valves equal or unequal; (5) branching pattern isotomous versus pseudomonopodial with distal isotomy possible; (6) aerial branch systems spiralled or planar; (7) axillary tubercles present versus absent or presence of other lateral branch-related projections; (8) non-vascularized emergences present versus absent. Some of these are included in the phylogenetic
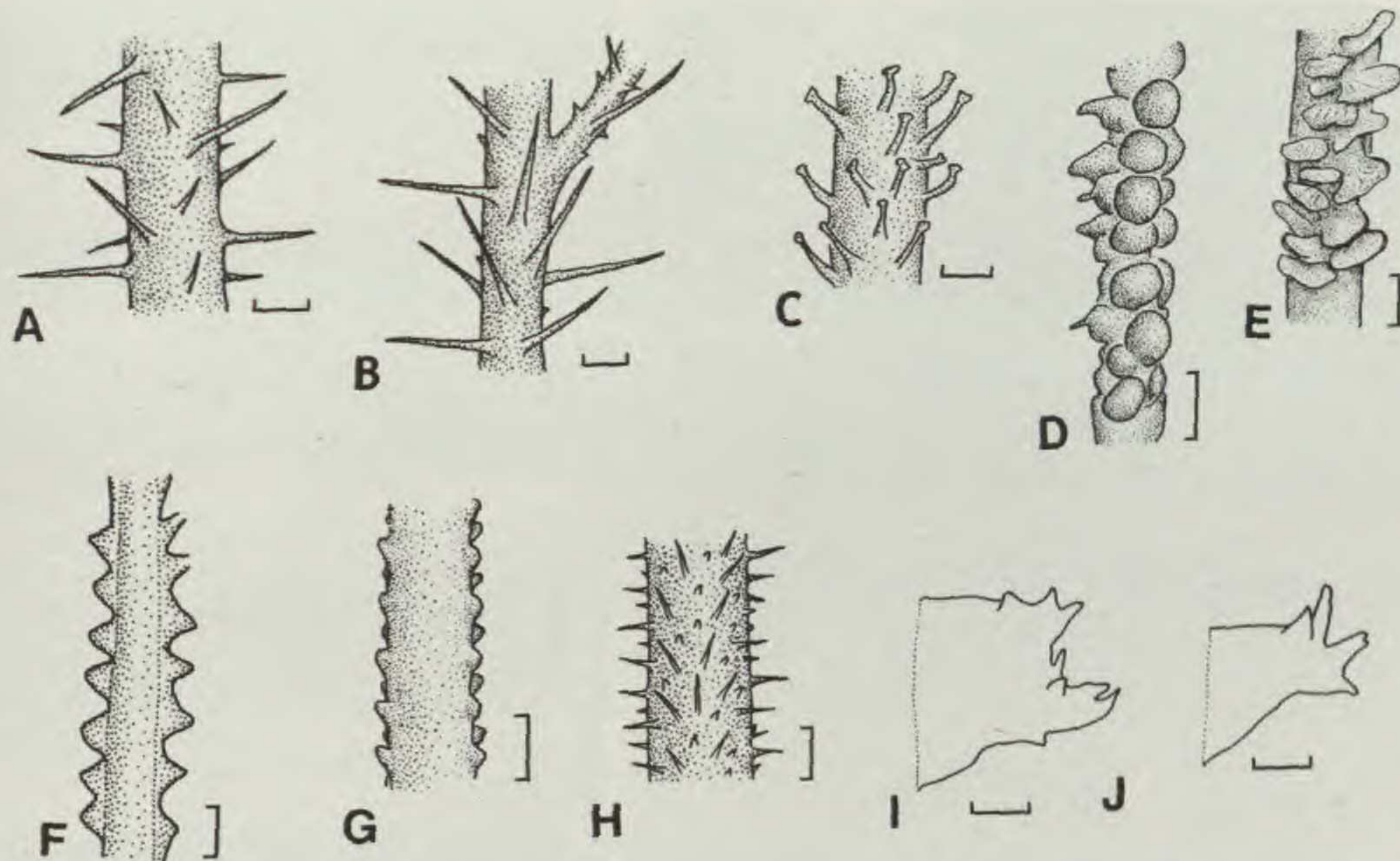
Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
Zosterophylls and Lycopsids

457

FIGURE 6. Line drawings interpreting emergence types in zosterophylls.—A. *Sawdonia ornata.*—B. *Koniora andrychoviensis.*—C. *Discalis longistipa.*—D. New zosterophyll type a.—E. New zosterophyll type b.—F. *Serrulacaulis furcatus.*—G. *Crenaticaulis verruculosus.* Papillae not shown. H–J. *Sawdonia acanthotheca.*—H. Unforked, spinelike emergences.—I., J. Forked emergences. A–H scale bars = 2 mm. I, J scale bars = 0.2 mm.

analysis discussed later, while others are too incompletely known or represent autapomorphies and could not be included as markers of phylogenetic relationships.

Emergence type is not in the above list and is excluded from the analysis to follow, because it is quite variable and autapomorphic. Several genera lack emergences entirely (*Zosterophyllum, Gosslingia, Tarella, Oricilla*). Among those with emergences, some have axes and sporangia covered with emergences while others exhibit distinct patterns such as opposite double rows in *Crenaticaulis*, or opposite and in single rows in *Serrulacaulis* (Fig. 6). The importance of emergences as a taxonomic character varies; considering several plant groups, in some cases it is used at the generic level (*Sawdonia*, the monotypic genera *Serrulacaulis, Crenaticaulis*), in others to distinguish species (*Psilophyton, Anisophyton*).

Banks (1968) and Banks & Davis (1969) proposed dividing the subdivision Zosterophyllophytina into two families, the Zosterophyllaceae and the Gosslingiaceae. Hueber (1972), Edwards (1970), Gensel et al. (1975), and several other workers have questioned whether this proposal was reasonable, and as more taxa have been added to the subdivision, it has been dropped, with the family Zosterophyllaceae being retained.

A recent assessment of characteristics of zosterophylls led Niklas & Banks (1990) to propose that two major types of zosterophylls could be recognized. One is characterized by axes that terminate in sporangia (terminate axes) and exhibit predominantly radial symmetry (although symmetry varies greatly in some taxa included here). *Zosterophyllum, Rebuchia*, and *Hicklingia* represent this group. The other type is characterized by axes not terminating in sporangia and exhibiting predominantly bilateral symmetry and encompasses the remainder of genera. Associated with this latter group is the presence of emergences, circinate axes, and possibly planar branching. The nonterminate character is somewhat problematic because axes are incomplete for several taxa included in that group. The proposition that emergences and sporangia are homologous to each other in the nonterminate group also needs further consideration, in part because sporangia can bear emergences.

Niklas & Banks (1990) suggest that the two types still are closely related, as only minor morphogenetic change is necessary to derive the second type from the first. Further, they propose that lycopsids arose, via the "pre-lycopsid complex," from the second type of zosterophyll, with a major reversal in symmetry (bilateral to radial). These hypotheses are worth further testing in that they are based on a dynamic concept of developmental aspects of the plants, and they build on previous observations concerning symmetry of sporangial arrangement and branching of several types of zosterophylls.

MORPHOLOGIC FEATURES OF PRE-LYCOPSIDS AND LYCOPSIDS

As previously noted, Gensel & Andrews (1984) and other workers have used the term "pre-lycop-

Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
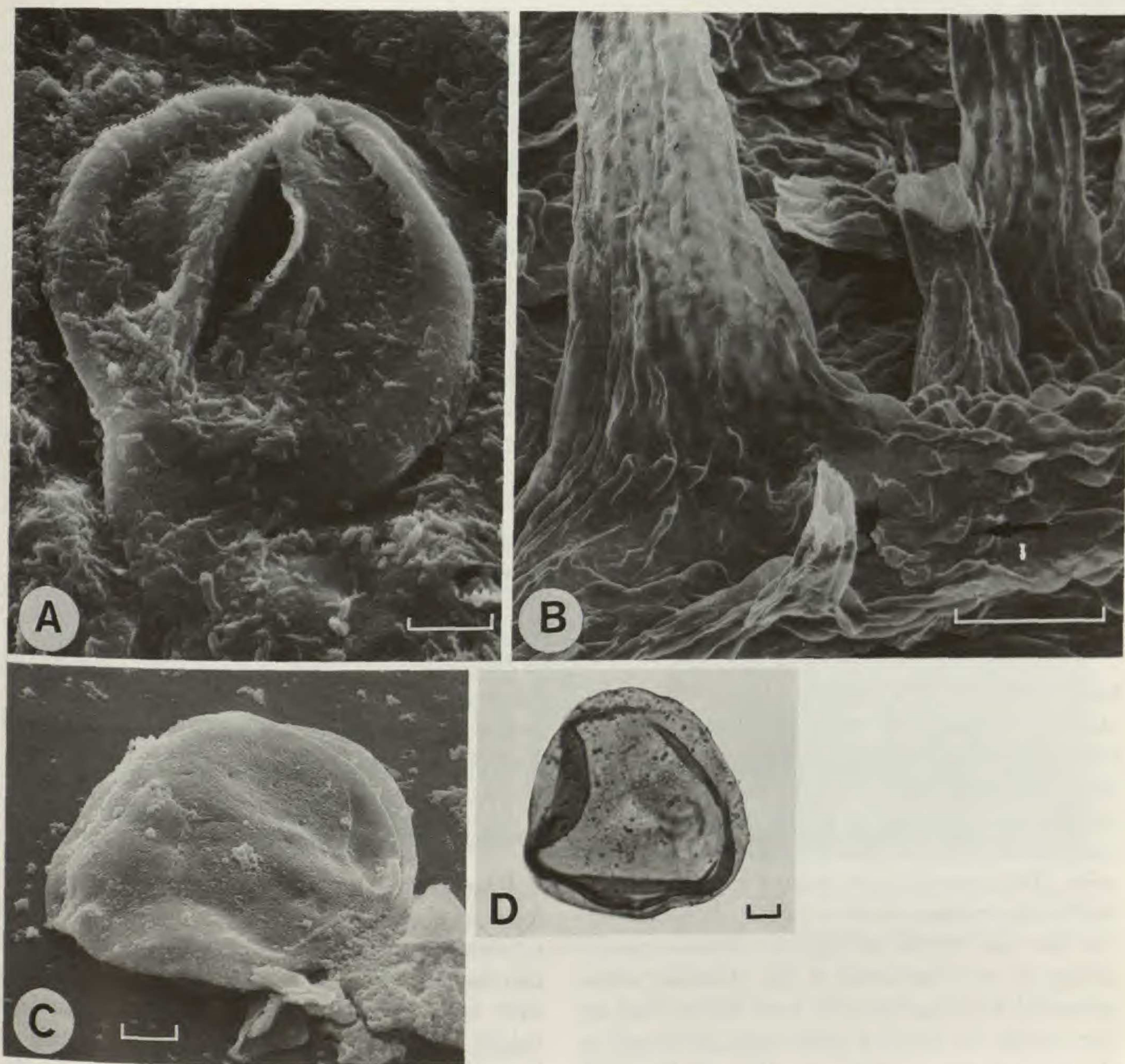Zosterophylls and Lycopsids

459
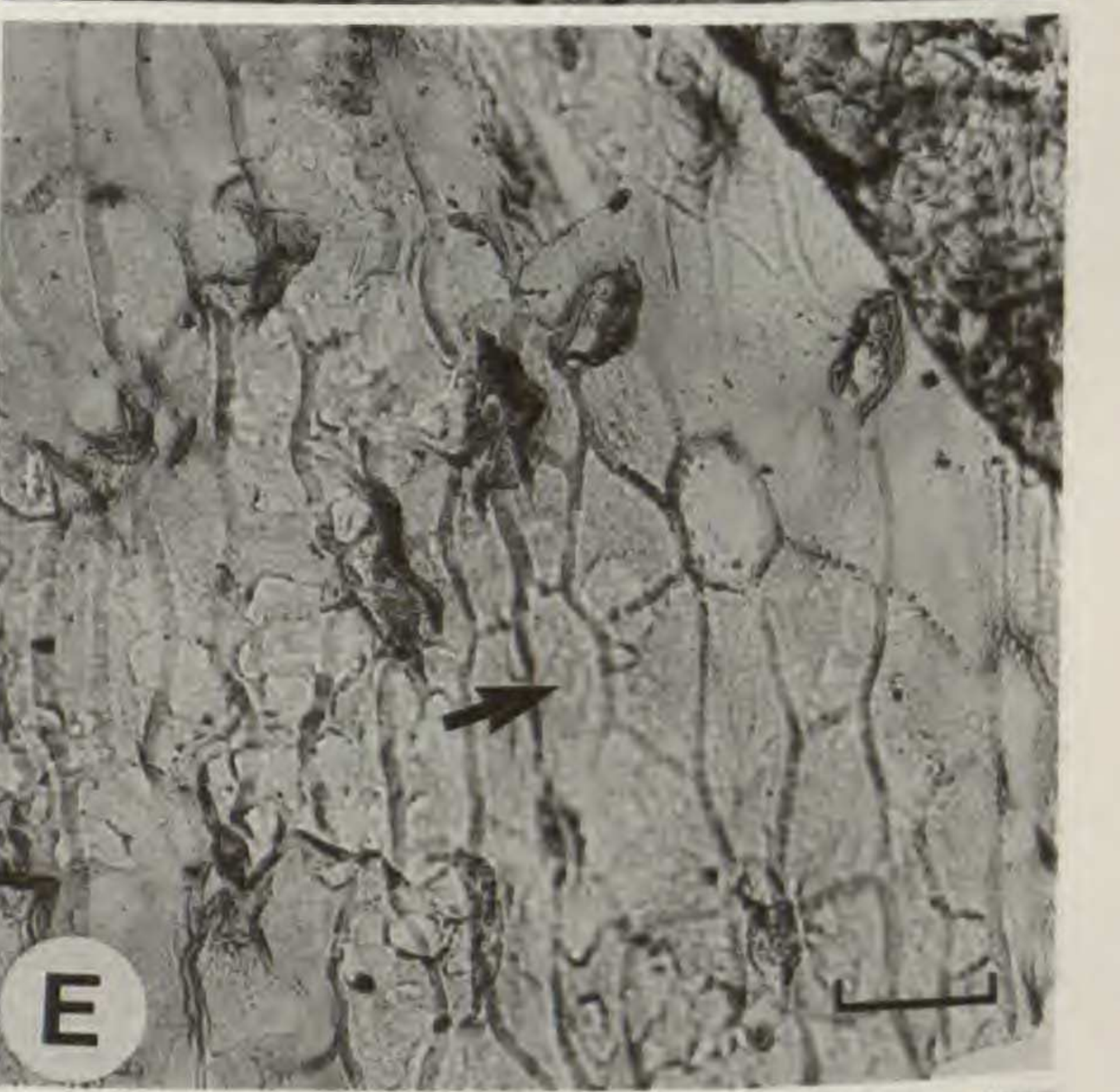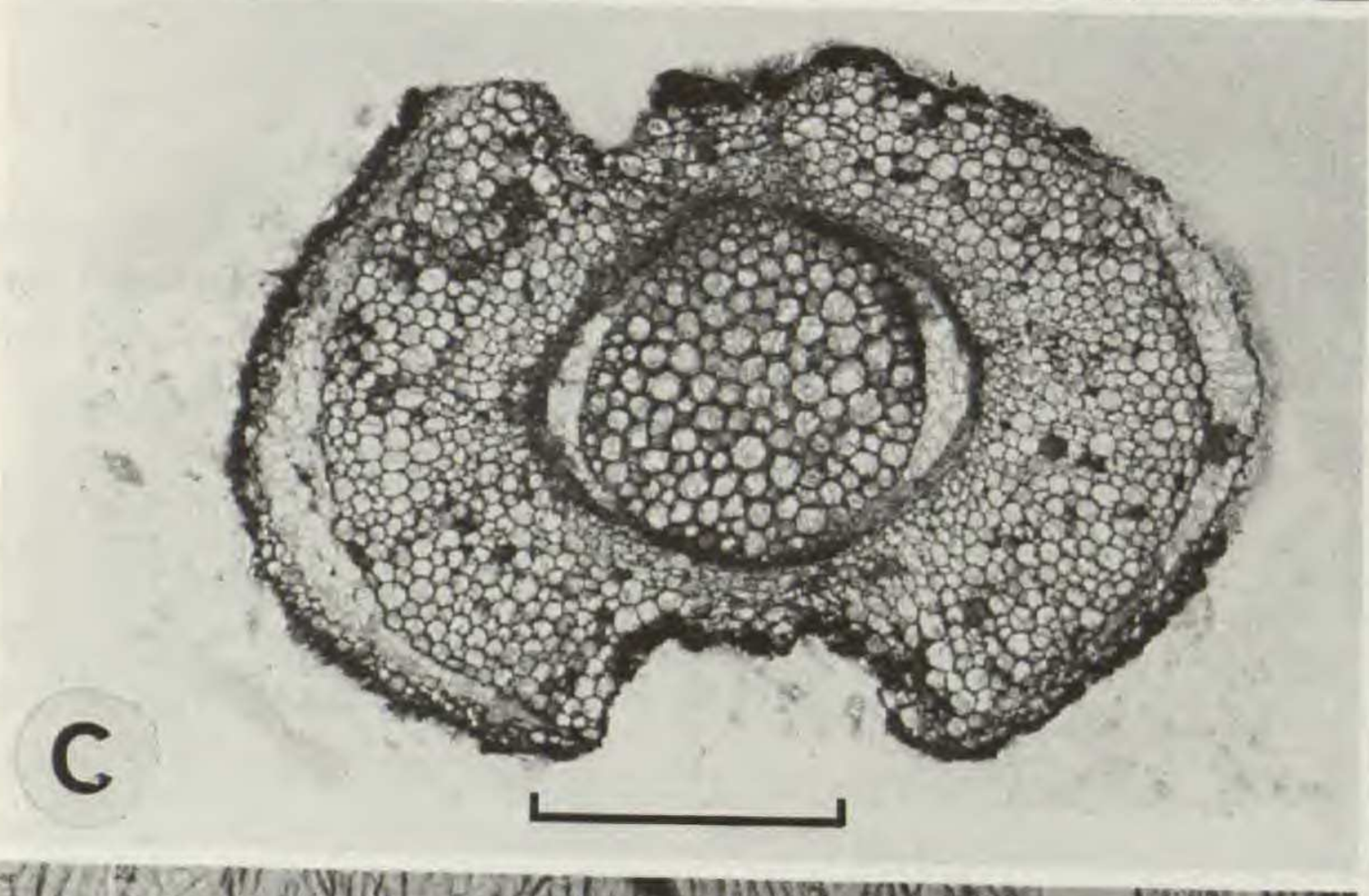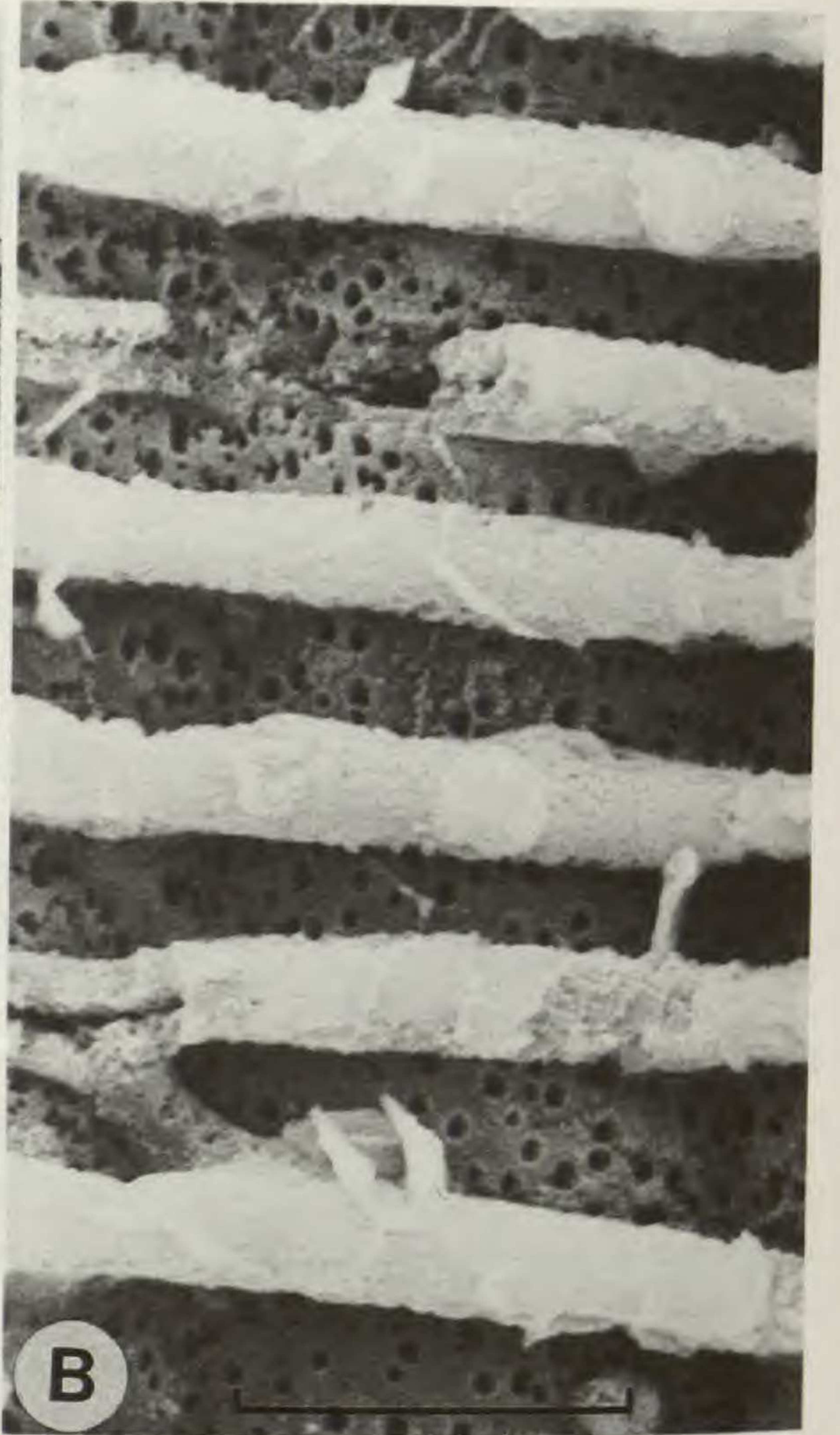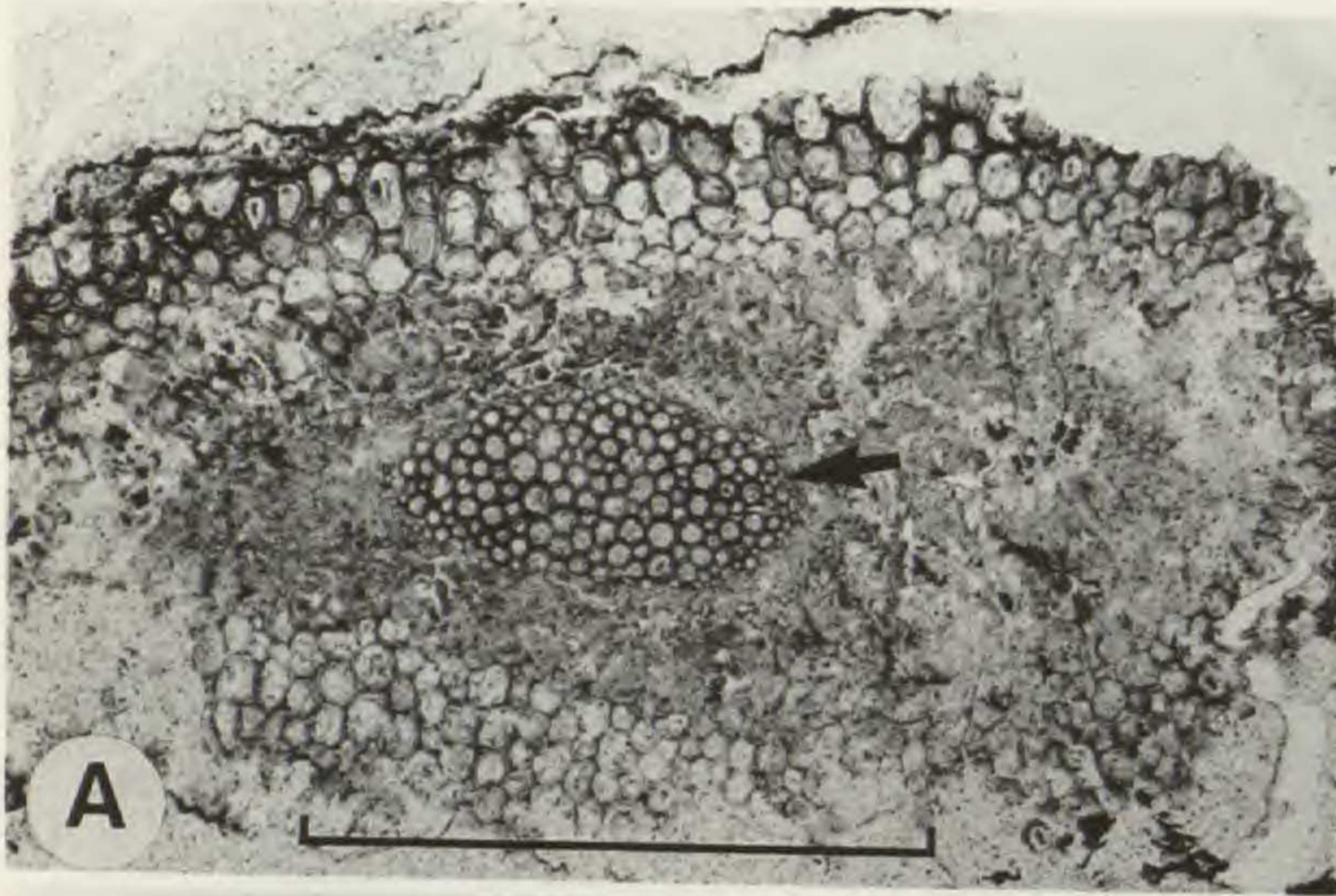
FIGURE 8. Cuticular and spore features of zosterophylls.—A. SEM of stomate of *Sawdonia ornata*, viewed from the inside. Ridge may be region where guard cells connect.—B. SEM of stem surface showing papillae and spine bases of *Sawdonia ornata.*—C, D. SEM and light micrograph (LM) of spores obtained from *Zosterophyllum divaricatum* sporangia. Note curvaturae, chagrenate surface. A, C, D scale bars = 10 μm. B scale bar = 100 μm.

sid" for some Devonian taxa (*Asteroxylon, Drepanophycus, Kaulangiophyton*) that are believed to be close to lycopsids in most of their characters but lack either a vascularized leaf or leaf-associated sporangia. They all are similar in exhibiting a rhizomatous habit, with prostrate axes producing aerial ones by dichotomy. The latter two exhibit H and K branching, and *Asteroxylon* and *Drepanophycus* bear adventitious roots (zosterophylls probably have these too). All of these taxa differ from

←

FIGURE 7. Anatomical and cuticular features of zosterophylls.—A. Cross section through stem of *Crenaticaulis verruculosus.* Note thickened cells in outer cortex and elliptic, exarch haplostele. An arrow indicates presumed protoxylem.—B. SEM of tracheid of *Crenaticaulis* in longitudinal view. This has directly and indirectly connected annular to helical thickenings and a perforated secondary wall in between.—C. Cross section of a stem of *Stolbergia* from the Middle Devonian of Maine illustrating an exarch haplostele, suggesting this plant may be a zosterophyll.—D. Cuticle of *Sawdonia ornata* showing papillate epidermal cells, stomata (s), and rosette cell pattern (r).—E. Cuticle of *Crenaticaulis verruculosus*—note the rosette cell pattern at the right.—F. Stomate of *Sawdonia ornata.* A, C, D scale bars = 1 mm. B scale bar = 10 μm. E, F scale bars = 0.1 mm.
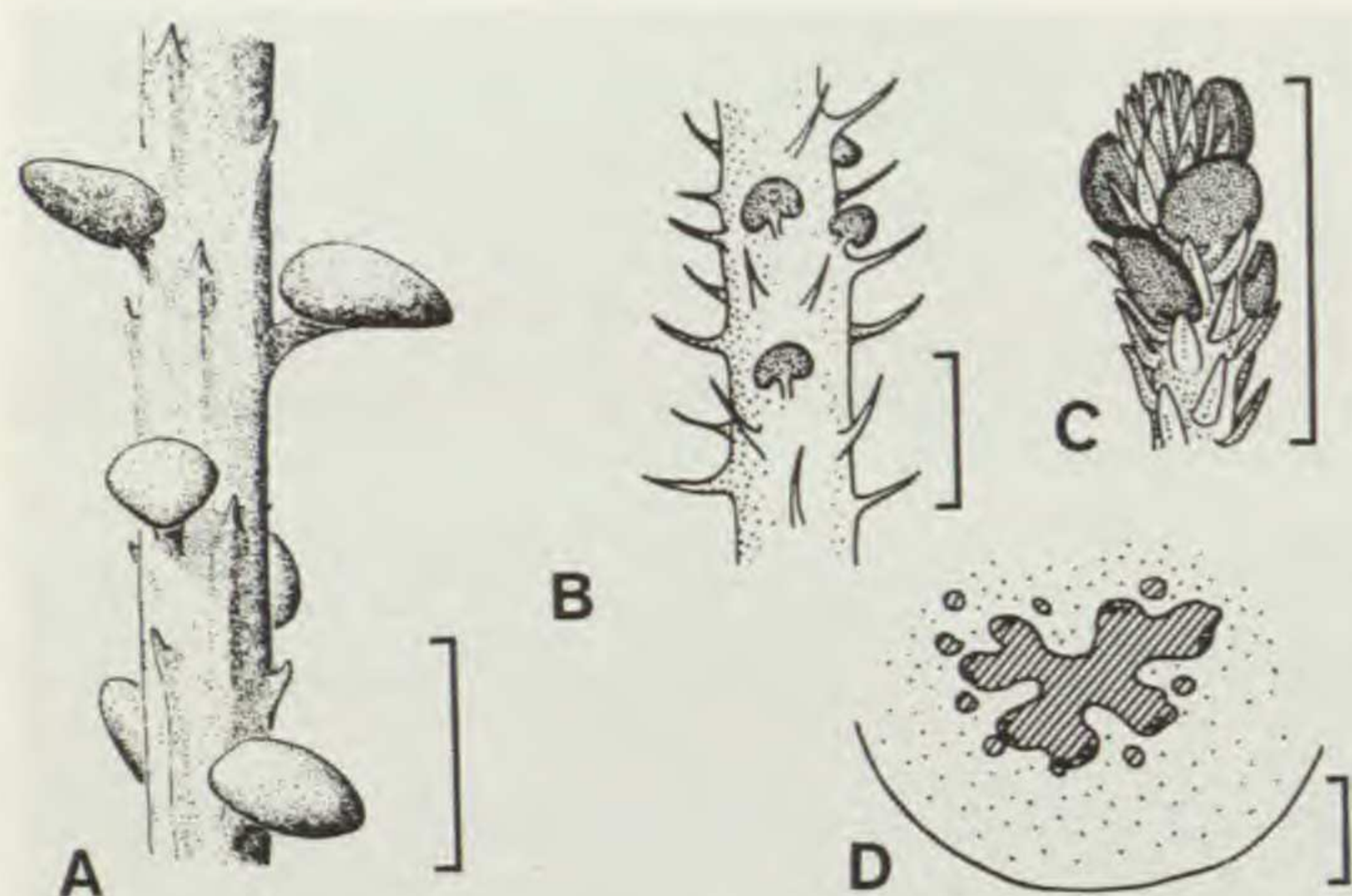
FIGURE 9.   Line drawings of pre-lycopsids.—A. *Kaulangiophyton akantha.*—B. *Drepanophycus spinaeformis.* C, D. *Asteroxylon mackiei.*—C. Restoration of "leafy" shoot with sporangia interspersed among "leaves."—D. Diagram of actinostele with traces. A redrawn from Gensel et al. (1969); B modified from Schweitzer (1980); C, D redrawn from Chaloner and MacDonald (1980). A–C scale bars = 10 mm. D scale bar = 1 mm.

lycopsids in that their sporangia are cauline, i.e., attached to stems by short stalks (Fig. 9A–C), rather than being associated with microphylls. *Asteroxylon* and *Drepanophycus* exhibit deeply lobed actinosteles (Fig. 9D) from which lateral traces emanate; anatomy is unknown for *Kaulangiophyton*. The lateral traces extend to the base of leaflike appendages in *Asteroxylon.* *Drepanophycus* has vascularized microphylls. There is no evidence of vascularization in the thornlike emergences of *Kaulangiophyton*, even though they are very similar to those of some axes attributed to *Drepanophycus spinaeformis* (Fig. 10A). Circinate axes are not evident. The sporangial stalks of *Asteroxylon* are vascularized.

Baragwanathia traditionally is considered the oldest undoubted lycopsid, exhibiting a deeply lobed actinostele with lateral traces supplying microphylls. Its sporangia have been presumed to occur in the axils of the microphylls, but sporangial attachment could be cauline as noted previously. There is no evidence of a stalk. The sporangia apparently occur in zones along the stem, and both microphylls and sporangia are radially arranged. At the very least, *Baragwanathia* is more similar to lycopsids than the preceding taxa, in that sporangia seem to be associated with leaves.

Leclercqia and several other genera present in Middle and Upper Devonian sediments are the best known early lycopsids (Fig. 11). These plants have exarch protosteles exhibiting ridges or variable depth of lobing, microphyllous leaves, and sporangia (where known) located adaxially on microphylls (Fig. 11B). Early lycopsids vary mostly in leaf

morphology, with those of *Leclercqia, Protolepidodendron scharyanum,* and *Colpodexylon* being five, two, and three times forked, respectively. Sporangia are attached to a small pad of sterile tissue on the microphyll surface. In *Leclercqia,* the attachment site is located near one end of the sporangium and is only one cell layer thick. Bonamo et al. (1988) did not recognize *Leclercqia* sporangia as stalked. However, when coding aspects of sporangial attachment for cladistic analysis, I regarded such pads in lycopsids as homologous to stalks.

Other lycopsids, such as *Haskinsia* and *Archaeosigillaria,* exhibit leaves with a distinctive shape (sagittate) or lobing (Fig. 11C, D). Their fertile parts are unknown. Many Middle Devonian lycopsids are much larger than most zosterophylls, although *Baragwanathia* and *Drepanophycus* can have axes 3 cm or more wide. Small tree-sized lycopsids appear by Late Devonian times. By the Carboniferous, a trend toward greater size and arborescence in some lineages, protection of sporangia, and their aggregation into strobili was well established.

POSSIBLE ANCESTRY OF ZOSTEROPHYLLS

It has been suggested that the zosterophylls arose from a rhyniophyte ancestor, although Banks (1968) did not indicate a relationship between the two lineages. Such a derivation would involve a shift from terminal to laterally borne sporangia (which could result from increasingly anisotomous branching) and from centrarch to exarch protoxylem maturation. How the latter might have occurred is unclear, especially in apparently "leafless" plants, unless by means of a change in developmental cues such as hormone distribution. Considering protoxylem maturation sequences among fossil and extant pteridophytes, I cannot think of any instances where such a shift has been documented. The closest might be in the changes in relative position of proto- and metaxylem in the so-called shoot-root transition zone in seed plants, where metaxylem differentiation changes from centripetal to laterally divergent to centrifugal in the zone between root and cotyledons (Esau, 1965).

Chaloner & Sheerin (1979) modified this scenario slightly to suggest both zosterophylls and rhynialean rhyniophytes may have arisen from *Cooksonia.* They further suggested that lycopsids arose from some zosterophylls and trimerophytes arose from rhyniophytes. Taylor (1988) noted that plants now included in *Cooksonia* may encompass vascular and nonvascular plants and suggested that
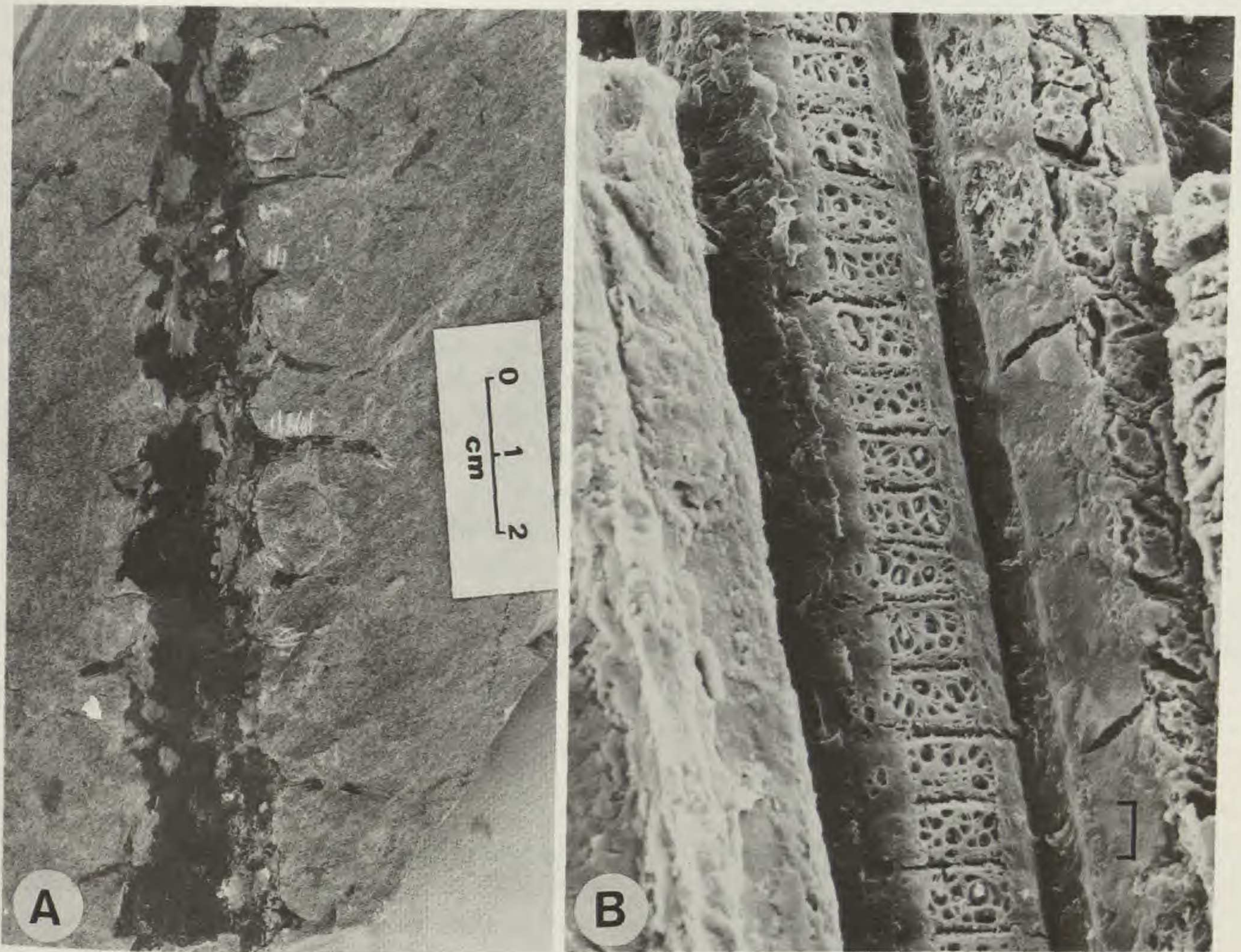
FIGURE 10. A. General view of *Drepanophycus spinaeformis* leafy stem. Leaves are long, falcate, and spinelike. Unfortunately, this specimen does not show leaf venation.—B. SEM of tracheid of cf. *Drepanophycus gaspianus* from New Brunswick, illustrating perforated secondary wall between scalariform thickenings. B scale bar = 10 μm.

the origin of zosterophylls, rhyniophytes, trimerophytes, and the major groups of bryophytes centered on a cladistically unresolved complex of poorly understood, highly variable plants with either no conducting cells or ones lacking secondary wall patterns—his so-called cooksonioid complex. This scenario obviates the need to explain a shift from centrarchy to exarchy and also implies the possibility of polyphyletic origin of conducting cells and possibly of tracheophytes. Unfortunately, no putative lineage in his study was supported by specific characters or character-state transformations (but see Kenrick & Crane, 1991).

Current research also has resulted in questions concerning which plants truly conform to the definition of a rhyniophyte. Edwards & Edwards (1986) adopted a fairly broad definition of rhyniophytes, especially in terms of types of branching pattern, but retained two original features, the occurrence of sporangia terminating infrequently branched axes and a centrarch haplostele. Taxa included in rhyniophytes by them are *Rhynia gwynne-vaughanii*, *Renalia*, *Taeniocrada decheniana*, and some

specimens assigned to *Aphyllopteris*, *Hostinella*, and *Taeniocrada*. *Uskiella* Shute & Edwards, 1989, may also represent a rhyniophyte.

Other plants originally assigned to the rhyniophytes either lack tracheids with obvious secondary wall patterns or are problematic with regard to some necessary characters. The major issue is how to define a tracheid, and thus a tracheophyte. Currently, the presence of lignified secondary wall thickenings is regarded as distinctive of tracheids. In such plants as *Aglaophyton*, *Nothia aphylla*, *Taeniocrada dubia*, and more recently, *Rhynia gwynne-vaughanii* (coded in this paper as a vascular plant), it is difficult to determine if the absence of secondary thickenings, or the presence of other types of patterns or wall layers, is an intrinsic feature or the result of preservational factors. These differences have been interpreted as intrinsic in many of these taxa and not homologous to tracheids, and all of these taxa except *Rhynia gwynne-vaughanii* have been formally removed from the rhyniophytes. Recent studies of Kenrick & Crane (1991) suggest that the conducting cell structure
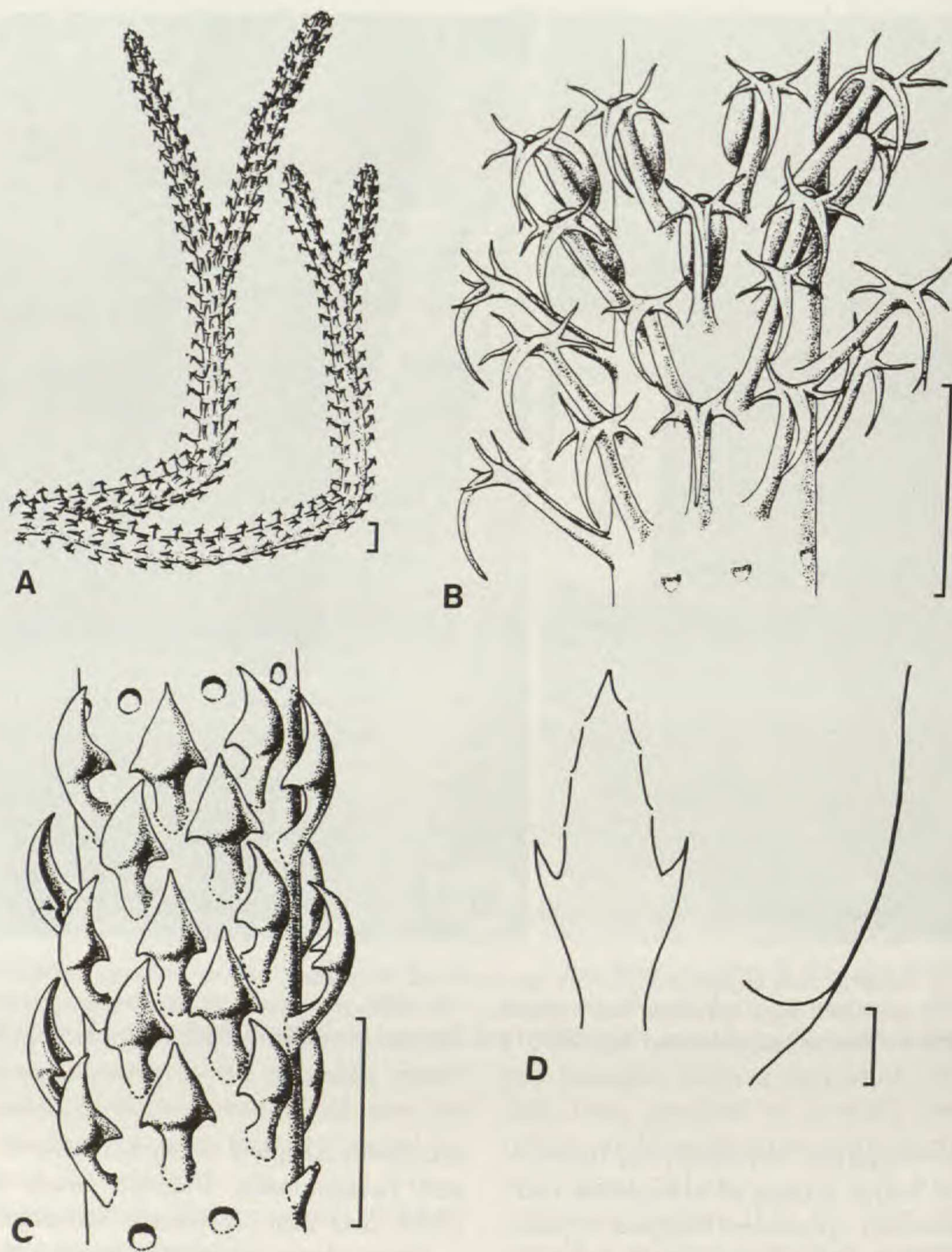
FIGURE 11. Line drawings of early lycopsids.—A. *Leclercqia complexa*, general habit.—B. Detail of *Leclercqia complexa* showing sporophylls and abaxial sporangia.—C. *Haskinsia colophyllus* showing sagittate leaves.—D. Diagram of leaf in front and side view of *Archaeosigillaria vanuxemii*. A–C redrawn from Bonamo et al. (1988). D redrawn from Fairon-Demaret & Banks (1978). A–C scale bars = 5 mm. D scale bar = 1 mm.

in *R. gwynne-vaughanii* also is more similar to *Sennicaulis* and *Taeniocrada*, and they present hypotheses concerning the possible affinities of these taxa. This obviously is important in considering rhyniophytes as a sister group or source of ancestor for any plant lineage and in assessing homology among conducting cells.

PATTERNS OF DIVERSIFICATION AND MORPHOLOGIC VARIATION

Examining the diversity (Fig. 1) of the zosterophylls and lycopsids shows that zosterophylls clearly diversified in the Siegnian–Emsian, with more than 14 genera represented, whereas the number of lycopsids present prior to the Middle Devonian is very low, being one or two, with an increase in numbers in the Middle and Upper Devonian. A few zosterophylls are recorded in the Eifelian–Givetian (*Hicklingia*, perhaps *Stolbergia*, *Euthursophyton hamperbachense*) and a few genera extend into the Upper Devonian (*Sawdonia*, *Serrulacaulis*, *Drepanophycus*). Thus, no matter when the group first appeared, diversification of lycopsids, on the basis of present evidence, lagged behind that of zosterophylls. The reason is unknown. Per-

Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
Zosterophylls and Lycopsids

463

haps early members were somehow constrained by ecological parameters (e.g., competition for the same habitat?).

There are some parallels in morphologic variation between the two groups. Emergences in zosterophylls and microphylls in pre-lycopsids and lycopsids are quite variable. Both may have performed similar functions—i.e., protection of the stem from desiccation, mechanical damage, or herbivory, and increased surface area for photosynthesis and gas exchange. It is assumed that vascularized microphylls would be more efficient both in providing water for photosynthesis and in transporting photosynthate away from its source. Early and Middle Devonian lycopsids are more or less similar in size to zosterophylls, but some younger lycopsids are much larger.

Sporangial attachment is different in the two groups, ranging from cauline, with vascularized stalks (in some zosterophylls at least, and *Asteroxylon*), to foliar, either axillary or epiphyllous (lycopsids). In some lycopsids, sporangial stalks are unvascularized. In younger lycopsids, sporophylls are modified to enclose sporangia more completely and differ anatomically. For example, sporophylls of some extant *Lycopodium* species have a mucilage cavity at their base or adjacent to the vascular strand (Bruce, 1976). Its function is unknown but might be to aid in moisture retention, store excess metabolites, or to aid spore dispersal by causing the sporophyll to reflex when dried. Sporangial stalks, although unvascularized, show patches of lignified cells (probable transfusion tissue) that are in contact with those surrounding the vascular strand of the sporophyll (Sykes, 1908). The ligule in extant *Selaginella* is regarded as aiding in moisture retention during early ontogeny or producing mucilage (Bilderback, 1987). The outer sporangium wall often is lignified.

Although anatomy is known for only about two-thirds of the zosterophyll genera, it is stereotypical, differing only in shape (terete or ellipsoidal to strap-shaped), which may correlate with arrangement of branches and/or sporangia. Anatomy in lycopsids varies mainly in depth of lobes, from deeply lobed to slightly ridged actinosteles. Tracheary wall patterning is circular to oval pitted in *Leclercqia* in contrast to the indirectly connected annular or helical patterns of most zosterophylls (*Koniora* also exhibits reticulate pitting) and pre-lycopsids. Tracheid diameter is similar in zosterophylls and lycopsids of comparable age, or in some cases greater in zosterophylls (Niklas, 1984). By the Middle Devonian, xylem cross-sectional area is greater in lycopsids than in zosterophylls, which might suggest

increased water-conducting capacity (Niklas, 1984, 1985).

Nothing is known about the gametophytes of zosterophylls (Schweitzer (1979, 1983) has suggested that a *Sciadophyton* may be the gametophyte of *Zosterophyllum*, but definite proof is lacking) or of extinct Devonian lycopsids other than their spores. The only notable difference in spores of homosporous Devonian members of the two groups is that those known in *Leclercqia* have a coarser ornament. Some Devonian lycopsids (e.g., *Cyclostigma*) are heterosporous, a reproductive syndrome not present among zosterophylls.

To what extent might these morphological differences lead to different evolutionary pathways? The lycopsids survived and zosterophylls did not. Is this chance, or might lycopsids have had a greater developmental potential? Did their more integrated and extensive vascularization confer survival advantage? No clear answers exist, but these questions should be pursued.

ECOLOGICAL PATTERNS

Evidence thus far does not suggest major differences in the habitat preferences of zosterophylls and lycopsids during the Devonian. Sedimentological analyses of plant-rich strata suggest both groups inhabited floodplain or channel margin environments, usually adjacent to streams or lakes. Within a deposit, a taxon may be represented by abundant, parallel aligned axes, or by closely intermingled specimens. Thus, it seems likely that they formed dense stands and that many were buried at or close to their site of growth. *Tarella* Edwards & Kenrick, 1986, is interpreted as living on an exposed point bar subjected to periodic flooding, which preserved parts of the stand during each episode. *Sawdonia ornata* in Gaspé occurs in a sandstone containing marine fossils immediately below the plant-rich layer; the sedimentary environment thus is interpreted as representing a tidally influenced floodplain (D. Lawrence, pers. comm.). *Leclercqia* is regarded as inhabiting a more distal floodplain habitat (Banks et al., 1985). The distribution of fossils in several Early and Middle Devonian deposits suggests only one type occurred in any given area; perhaps in the Lower Devonian, zosterophylls, pre-lycopsids, and *Leclercqia* competed for similar sites, and only one type predominated as might be expected of clonal or "turfing-in" types of organisms.

Edwards & Kenrick (1986) suggested that the occurrence of dormant apices (subaxillary protuberances of various degrees of development) may have been an adaptation to unstable environments,

allowing the plant to begin growing again after damage (or partial burial) or to become reestablished after being uprooted. Zosterophylls also show some cuticular features that could be interpreted as adapted for periodic water unavailability, for example: (1) their cuticles are quite robust and resistant to destruction (in contrast to those of trimerophytes or rhyniophytes); (2) many exhibit epidermal cells with papillae (thickened regions of cuticle); and (3) their stomata in some cases appear sunken (*Sawdonia, Deheubarthia*). Several also exhibit the distinctive, epidermal "rosette cell" arrangement (Fig. 7D, E), which has been considered to represent either hair bases (although hairs never have been seen), mini-lenses for concentrating sunlight for photosynthesis (Rayner, 1983), an unknown function in plant water relations (Edwards et al., 1982), or salt glands. *Drepanophycus* often has a very large diameter axis with a narrow vascular strand, leading to the suggestion that it was possibly succulent.

EVOLUTIONARY CONSIDERATIONS

Despite abundant new evidence, particularly of zosterophylls and earliest land plants, it still is not possible to resolve how microphylls and leaf-associated sporangia arose. Evidence from fossil plants and extant lycopsids seems to favor the vascularization of enations theory more extensively than the telome reduction theory (see also Niklas & Banks, 1990). The presence of forked microphylls in some early lycopsids is not necessarily problematic because they too could have evolved from emergences. In a paper submitted elsewhere (Gensel, 1991), I demonstrate the occurrence of emergences that fork up to eight times in *Sawdonia acanthotheca*. One could suggest on that basis that the genetic potential for forked emergences existed in the putative ancestral plants, which could be co-opted or expressed during leaf development in some putative descendants.

The traditional views of the origin of foliar-associated sporangia are that either the sporangium became associated with the leaf through "phyletic slide," perhaps via developmental changes that reduced the distance between leaf and sporangium, or through modification of a branch truss with both vegetative and fertile components (the telome theory).

Evidence supporting either of these hypotheses is inconclusive. Reports concerning development of sporangia in extant lycopsids are conflicting; in some cases the sporangial initials originate on the stem and in others on leaves (Eames, 1936). Sykes

(1908) noted that sporangia primordia in *Lycopodium selago* originated separately from leaf primordia, the developing sporangia becoming associated with leaves later. Bower (1935), however, described sporangial initiation as foliar for the same species. Eames also noted that where sporangia originate is not necessarily where they are located at maturity, although those originating on leaves usually stay positioned on leaves. Additional studies of sporangial and leaf development in extant lycopsids are needed to clarify this variability. Such studies might shed light on how the lycopsid sporangium/sporophyll affiliation came about. If the sporangium-leaf association is variable in extant lycopsids, the same might apply to fossil ones. This is significant in regard to the status of *Baragwanathia*; simply having leaf-associated sporangia may be sufficient to place it in the lycopsids without worrying about whether it attaches to the stem or the leaf.

Another explanation for the transition from cauline to foliar-borne sporangia might be heterotopy. A displacement of meristematic activity producing lateral appendages (sporangial primordia) from stem apex to leaf axil or leaf surface would result in the establishment of leaf-associated sporangia. This same process also could be invoked to explain forked emergences or microphylls. Heterotopy is considered the probable cause of epiphyllous leaves in *Begonia* by Sattler & Maier (1977). Other examples are reviewed by Sattler (1988).

Are microphyllous-associated sporangia homologous with those borne on stems or megaphylls? I have assumed so, since both originate from cauline structures. Therefore, the sporangial stalk of all zosterophylls is regarded as homologous to a stem in the phylogenetic analysis. Sporangial stalks in lycopsids also are homologous to stems, but seem to have lost vascular tissue. This phylogenetically important assumption requires further investigation.

PHYLOGENETIC ANALYSIS OF EXTINCT AND EXTANT "PTERIDOPHYTES"

To evaluate phylogenetic relationships of zosterophylls, pre-lycopsids, and lycopsids more rigorously, I have initiated a phylogenetic analysis of selected fossil and living pteridophytes using cladistic methodology. The results presented here are preliminary. Further analysis is ongoing, and a fuller treatment will be presented elsewhere (Gensel, Mishler & Albert, in prep.).

Numerous problems exist in attempting to use fossils in cladistic analysis, as summarized by Don-

Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
Zosterophylls and Lycopsids

465

oghue et al. (1989), but their argument, which focuses on the importance of using fossils in phylogenetic analysis of living plants, can be inverted and used to support inclusion of living taxa in phylogenetic reconstruction of fossil taxa. Discussions of the benefits and problems involved in attempting phylogenetic analysis of fossil plants via cladistics are well presented by Schoch (1986), Stein (1987), Stein & Beck (1987), Crane & Hill (1987), and Doyle & Donoghue (1987).

Problems that were faced here include some mentioned by the above workers, such as: (1) not all fossil remains present comparable sets of characters; (2) the plants mostly are of simple construction and present a comparatively low number of characters; and (3) developmental data are sparse or lacking. Combined, these result in the analysis being limited to a small set of putatively homologous characters. These problems are particularly acute when analyzing ancient lineages of land plants. In selecting characters, I attempted to include characters traditionally used in delimiting fossil and extant taxa at the generic and higher levels, but realize these represent hypotheses of homology that may be refuted as new knowledge is obtained. Because of the range of taxa, and the limitations of fossil remains, only a few character states could be judged homologous and synapomorphous (i.e., shared by two or more taxa). This limits the potential for accurate phylogenetic reconstruction because of the probable lack of resolution resulting from analysis of many taxa with few characters.

Wagner parsimony, PAUP 3.0d by D. Swofford, was used with a Macintosh computer to conduct the analysis. This program allows for coding multistate characters and for the construction of character state trees if needed. Three general modes of character evolution were used: (1) unordered, (2) ordered with linear transformational series, and (3) ordered with nonlinear transformation series (CSTREE option of PAUP 3.0d).

Twenty-five taxa and 12 coded characters were used to generate the cladograms. The taxa included genera of the major early land plant lineages, e.g., rhyniophytes, zosterophylls, the pre-lycopsids (*Asteroxylon* and *Drepanophycus*), *Baragwanathia*, *Leclercqia*, *Lepidophloios*, two extant species of *Lycopodium*, the trimerophytes *Psilophyton* and *Pertica*, the aneurophyte *Tetraxylopteris*, *Psilotum*, the extinct filicalean fern *Botryopteris*, and the extant marattialian *Angiopteris*. Taxa were selected that met one or more of the following criteria: (1) they represent a lineage, (2) they are well enough known that most of the characters can be coded, and/or (3) they are significant in evo-lutionary theories discussed previously. If a genus was polymorphic for the characters employed, a representative species was selected; thus, *Sawdonia* is based on *S. ornata*, *Drepanophycus* is based on *D. spinaeformis*, and *Botryopteris* is based on *B. antiqua*. In two cases, more than one species of a polymorphic genus was included in the data set (*Psilophyton*, *Lycopodium*). Some taxa were not included because they did not meet the above criteria. I included many more zosterophyll genera than for other lineages, because I wanted to test relationships within that group. Even so, some zosterophyll genera were omitted either because they are too incompletely known or because they score identically with a genus present in the analysis. A hypothetical moss ancestor, based on characteristics postulated by Mishler & Churchill (1985), was included in order to polarize characters.

Sporangial characters, branching patterns, and vascular anatomy distinguish not only major lineages of Devonian plants, but modern ones to some extent as well. These also are ones most readily obtained from the fossils; many of these characters are used in this analysis. However, branching patterns were difficult to code and resulted in character conflict; thus all aspects of branching except ones relating to how sporangia are borne on the plant were abandoned. Despite criticism for using characters that have questionably discrete states, I included one such character (sporangial shape) in these initial attempts since sporangial shape has been used to distinguish major groups of early land plants. Emergence shape and position are too variable (and either autapomorphous or homoplasious) to be included. Data on gametophytes, cuticular features, and spores are lacking, too incomplete, or not presently informative in the group as a whole. Of the 12 characters employed (Table 2), characters 3, 8, 9, and 11 were unordered. Character 2 was obtained as a branching character state tree, and the remainder were ordered with a linear transformation series. Explanation of these characters and their ordering follows next.

1. *Sporangial location.* Whether sporangia are attached to a stem or leaf and their location on a sporophyll distinguishes several plant lineages. Cauline sporangia occur in the hypothetical moss outgroup, rhyniophytes, zosterophylls, trimerophytes, pre-lycophytes, and aneurophytes. Other states, e.g., axillary or epiphyllous, are considered transformationally homologous on the premise that the sporangiophore in any tracheophyte is a cauline or cauline-derived structure. Epiphyllous sporangia are either abaxial or adaxial. Character 1 is thus linearly ordered a-b-c-d.

TABLE 2. List of characters used in this study and indication of type of ordering (O = ordered linear, U = unordered, CSTREE = ordering nonlinear). For details, see text.

1. Sporangial location (O)
   a. epiphyllous, abaxial
   b. cauline
   c. axillary
   d. epiphyllous, adaxial
2. Sporangial position if cauline (CSTREE)
   a. terminal on unbranched axis
   b. terminal on branched axis
   c. lateral, branched axis
   d. lateral, unbranched axis
3. Sporangial arrangement if cauline and lateral (U)
   a. spiral
   b. linear
   c. singly
4. Sporangial orientation (O) (stalk or dehiscence line relative to organ bearing it)
   a. upright
   b. horizontal
5. Sporangial shape (O)
   a. height greater than width
   b. globose
   c. width greater than height
6. Stem outgrowths (O)
   a. emergences absent
   b. emergences present, not vascularized
   c. emergences present, vascularized to base
   d. emergences present, fully vascularized

7. Megaphylls (O)
   a. absent
   b. present
8. Stelar type in mature state (U)
   a. Haplostele
   b. actinostele
   c. plectostele
   d. siphono- or dictyostele
9. Metaxylem wall patterning (U)
   a. absent
   b. annular-helical
   c. indirectly connected annular, helical
   d. scalariform to reticulate to some pitted
   e. mostly pitted, including bordered pitted
10. Xylem maturation (O)
    a. centrarch
    b. mesarch
    c. exarch
11. Tubercles, etc. (probably arrested apices) (U)
    a. absent
    b. present, scattered
    c. present, branch-related
12. Circinate axes (O)
    a. absent
    b. present

One can postulate a reasonable transformation series of sporangial location, from cauline to axillary to adaxial epiphyllous, or from cauline to abaxial epiphyllous, considering the range of positions evident among extant and fossil plants and incorporating some modification of the "phyletic slide" hypothesis (Bower, 1935). Derivation of adaxially borne sporangia as in lycophytes was discussed in a previous section; abaxially borne ones are considered to be parts of a branch system that became modified to form a megaphyllous leaf.

2. *Sporangial position, if cauline.* This is used to distinguish between plants with cauline sporangia in terms of whether they are borne at the tips of axes or laterally along axes. The states recognized are terminal on unbranched axes, terminal on branched axes, lateral on unbranched axes and lateral on branched axes. Starting with the simplest condition, terminal on unbranched axes, axis dichotomy could result in terminal on branched axes. Unequal dichotomies of axes could produce either branched or unbranched lateral units. Thus, this character is ordered as a branched character

state tree as follows: $a-b\substack{c \\ d}$. Following the scenario presented by Mishler & Churchill (1985) concerning transformation of sporophyte characters: the hypothetical ancestor of mosses + tracheophytes consists of a stalk and sporangium borne on the gametophyte thallus. Next occur independent sporophytes with branched axes, which subsequently become more elaborately branched. Unequal dichotomies within sporophyte axes might result in either sporangia borne laterally on branched axes or sporangia borne laterally on unbranched axes (stalks). From these can be derived the epiphyllous conditions coded in the previous character.

These first two characters were kept separate; any attempt to combine them into a more complex series of states resulted in constraining how states could change more than I deemed reasonable.

3. *Sporangial arrangement, if cauline and lateral.* This refers to the pattern of lateral sporangia, i.e., whether spiralled, linear (in two rows

Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
Zosterophylls and Lycopsids

467

TABLE 3. Data matrix for cladistic analysis.

Taxon	Character											
	1	2	3	4	5	6	7	8	9	10	11	12
Hypothetical moss outgroup	b	a	?	?	a	a	a	a	a	?	a	a
Zosterophyllum llanoveranum	b	d	a	a	c	a	a	a	b	c	b	a
Sawdonia ornata	b	d	b	a	c	b	a	a	c	c	b	b
Crenaticaulis verruculosus	b	d	b	a	c	b	a	a	c	c	c	b
Gosslingia breconensis	b	d	b	b	c	a	a	a	c	c	c	b
Thrinkophyton formosum	b	d	b	a	c	b	a	a	c	c	c	b
Koniora andrychoviensis	b	d	c	b	c	b	a	a	d	c	a	b
Tarella trowenii	b	d	b	b	c	a	a	a	c	c	b	b
Cooksonia sp.	b	b	?	?	b	a	a	a	b	a	a	a
Rhynia gwynne-vaughanii	b	b	?	?	a	a	a	a	b	a	b	a
Renalia hueberi	b	c	a	a	c	a	a	a	b	?	b	a
Drepanophycus spinaeformis	b	d	a	a	c	d	a	b	c	c	a	a
Asteroxylon mackiei	b	d	a	a	c	c	a	b	b	c	a	a
Baragwanathia longifolia	c	?	?	a	c	d	a	b	b	c	a	a
Leclercqia complexa	d	?	?	b	c	d	a	b	e	c	a	a
Lepidophloios sp.	d	?	?	b	c	d	a	d	e	c	a	a
Lycopodium lucidulum	c	?	?	b	c	d	a	c	e	b	a	a
Lycopodium clavatum	d	?	?	b	c	d	a	c	e	b	a	a
Psilophyton dapsile	b	b	?	a	a	a	a	a	d	a	a	a
Psilophyton charientos	b	c	a	a	a	b	a	a	d	a	a	a
Pertica sp.	b	c	a	a	a	b	a	b	d	b	a	a
Tetraxylopteris schmidtii	b	c	a	a	a	a	a	b	e	b	a	a
Psilotum nudum	b	c	a	a	b	?	a	d	e	c	a	a
Botryopteris antiqua	a	?	?	b	a	b	b	a	e	b	a	b
Angiopteris evecta	a	?	?	a	a	b	b	d	d	b	a	b

or in one row), or single. This has been especially in distinguishing zosterophyll genera, but also is useful when considering sporangial arrangement in other lineages. This character is unordered.

4. *Sporangial orientation.* This refers to the orientation of sporangial stalk and dehiscence line relative to the cauline or cauline-derived structure bearing the sporangium, as described earlier, i.e., are sporangia upright or horizontal? Indehiscent sporangia are coded with a question mark.

5. *Sporangial shape.* An attempt is made here to distinguish between plants bearing globose, reniform, or elongate (including fusiform) sporangia, because this is used in taxonomic delineation of major types of early Devonian plants. The distinctness of these states needs verification using quantitative methods. States include sporangium height greater than width, equidimensional (globose) or width greater than length. This morphocline was linearly ordered a-b-c. Sporangia that are higher than wide are regarded as basal, because that state is present in the hypothetical moss outgroup.

6. *Stem outgrowths.* This attempts to reflect some features used to differentiate within zoster-

ophylls, or between them and other lineages. The following character states are recognized and linearly ordered as presented: emergences absent, emergences present, emergences present and vascularized to their base, and emergences present and fully vascularized. Fern scales or trichomes are considered homologous to emergences. It should be noted that this transformation series reflects one prevailing hypothesis about how microphylls are derived, and thus does not follow Stewart's hypothesis that some lycopsid leaves are not derived from emergences. This will be examined in future studies, if possible. Ordering is a-b-c-d.

7. *Megaphylls.* Absence or presence of megaphylls was coded a-b, since megaphylls are regarded as derived via modification of lateral branch systems. It is possible that not all megaphylls are homologous; in this data set, however, the only megaphyllous plants are ferns and I regard their megaphylls as being homologous.

8. *Stelar type.* Character states include a haplostele (protostele with entire outline), actinostele, plectostele, and siphono- or dictyostele (these two differ only in the spacing of leaf gaps). Each of the latter types can be derived from a haplostele

separately. Thus, the character is unordered. The hypothetical moss outgroup, and earliest presumed tracheophytes, exhibit haplosteles.

9. *Metaxylem wall patterning.* The states coded here include absence of any pattern, then the following patterns: annular to helical, indirectly connected annular-helical, scalariform to reticulate to pitted, and mostly pitted including bordered pits. Because more than one pattern may occur within a single metaxylem element, and among metaxylem elements within one taxon, each state was broadly defined. Based on known developmental sequences in many tracheophytes, transformation from annular to scalariform, or annular to helical to scalariform is possible, as are other types of changes. Thus, this character is left unordered.

10. *Xylem maturation pattern.* Maturation is considered either exarch, mesarch, or centrarch (endarch is considered not applicable in this study). Changes from one state to another could involve one or two steps. The most logical series, i.e., centrarch to mesarch to exarch, is used here. The character is ordered a-b-c.

Conducting cells of some mosses are centrarch, others undetermined (Hébant, 1977). This character is not known in *Cooksonia* so it is coded as a question mark. Traditionally, rhyniophytes with centrarch protosteles are considered basal, giving rise to lineages with either exarch or mesarch ones. However, it is not clear how exarchy is derived from centrarchy or vice versa nor if an intermediate mesarch condition is necessary (no fossil evidence exists to support this). If vascular plants arose from a rhyniophytoid ancestor, either centrarchy or exarchy could be basal.

11. *Tubercles, etc. (arrested apices).* Included here are the tubercles, or axes that arise in the same position as tubercles, that occur in several plant groups and vary in location and morphology. They seem to reflect the inability of some shoot apices to continue development in these early land plants. There is no evidence of how states are related, and this character is left unordered.

12. *Circinate axes.* Stems of zosterophylls are circinate, as are leaves of most ferns. Even though involving different organs, they are homologous structures if fern megaphylls evolved from branch systems, and thus they are coded the same. A one-step change can be invoked here. Absence of circinate vernation is considered primitive since mosses and *Cooksonia* lack it.

Table 3 shows the resulting data matrix for the 25 terminal taxa. Question marks indicate unknown data or inapplicable character states. The computer algorithm assigns character states to "unknown" entries to give the minimal number of changes when mapped onto the topology based on known character states. One needs to consider whether missing or inapplicable data are critical in the case of these simple plants, especially in ones regarded as basal to major lineages. Specific examples in this analysis are: (1) tracheids are not known with certainty in fertile *Cooksonia* axes and vascular characters, thus are coded as a question mark for that taxon; (2) similarly, while tracheids are visible in cleared axes of *Renalia*, it is not possible to determine their maturation sequence; and (3) the present interpretation of the conducting cell pattern and conducting cell homology to tracheids in *Rhynia gwynne-vaughanii* may change (see Kenrick & Crane, 1991).

PAUP 3.0d was run with the following parameters: 10 random replications, TBR (Tree bisection-reconnection branch swapping) and NNI, ACCT-RAN, and MULPARS option. This resulted in 350 most parsimonious trees of 50 steps. One of the 350 most parsimonious trees is shown in Figure 12, with characters mapped on to indicate one way the various clades may be derived. The combinable component consensus tree is shown in Figure 13 and shows that most of the topology is retained. Some groups of plants are highlighted for ease of discussion, e.g., S = "*Sawdonia* clade" and A = "*Asteroxylon* clade" in Figure 12.

The consensus tree shows the following: (1) many nodes still require resolution, especially in the basal regions of the cladogram and among the plants traditionally considered as rhyniophytes, trimerophytes, ferns, and aneurophytes; (2) some parts of the tree support prevailing ideas about relationships of Devonian plants, but differences also appear; and (3) several monophyletic groups corresponding to prevailing systematic categories occur (pre-lycopsids/lycopsids; lycopsids plus zosterophylls; the ferns).

One lineage from the large basal polychotomy includes *Zosterophyllum*, the *Sawdonia* clade (rest of the zosterophylls included in this study), *Renalia*, and the *Asteroxylon* clade (pre-lycopsids and lycopsids). The position of *Zosterophyllum* as a separate line in relation to the rest of the zosterophylls (= *Sawdonia* clade) and the composition of the *Sawdonia* and *Asteroxylon* clades are constant in all trees, as are the relative positions of the pre-lycopsids. *Leclercqia*, *Lepidophloios*, and *Lycopodium* vary in their relationships, and this variation is shown in Figures 12 and 13. *Gosslingia* and *Tarella* form a clade, often sister to *Koniora*. The position of *Renalia* is variable (and in my opinion, problematical); it either appears as sister

Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
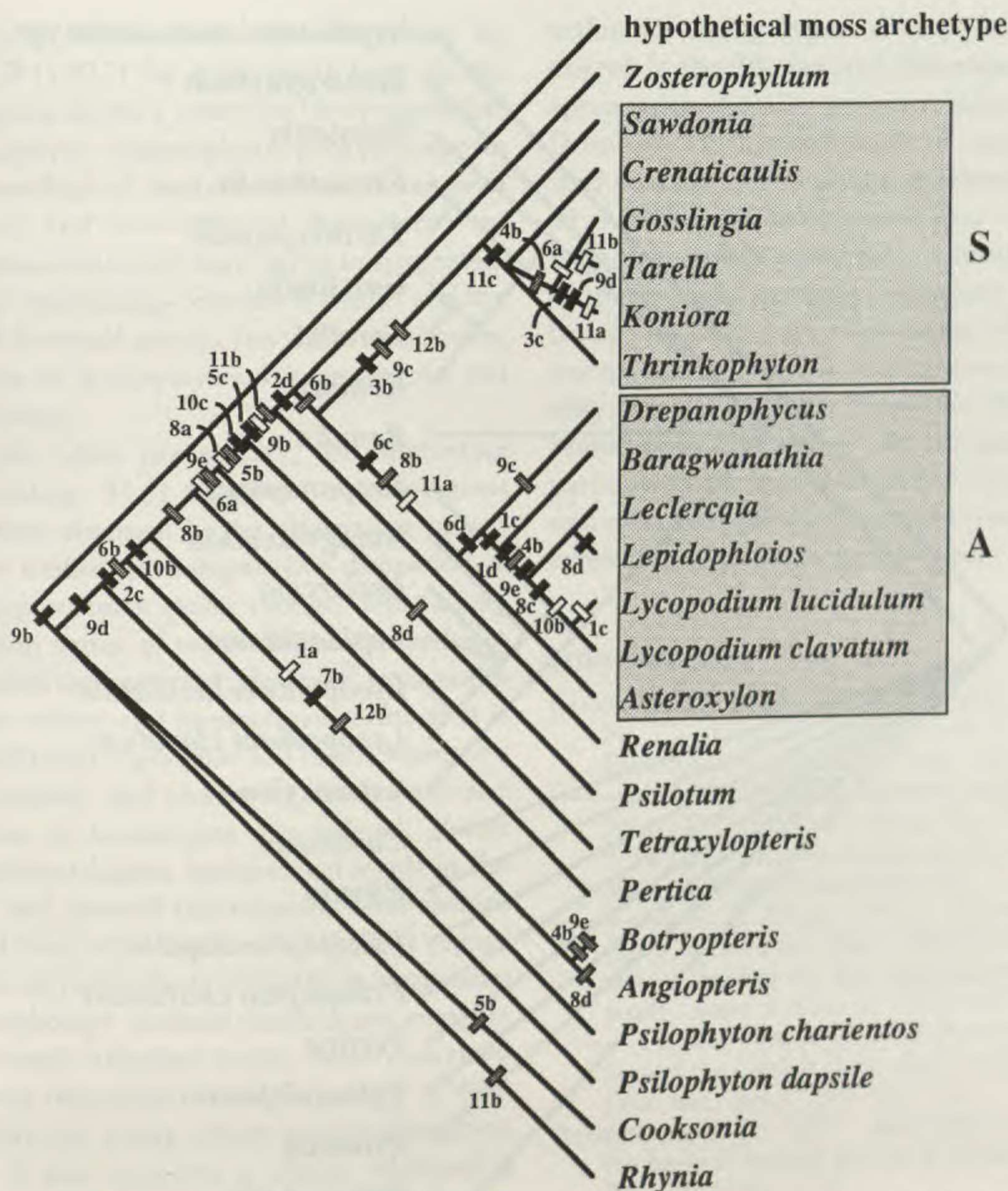Zosterophylls and Lycopsids

469

FIGURE 12. One of the 350 most parsimonious trees. Character states are mapped on as follows: dark rectangles indicate directional changes, stippled rectangles indicate parallelisms, and blank rectangles indicate reversals. Number and letter indicate character number and state to which it changed at that level. Categories such as *Sawdonia* clade are highlighted for ease of discussion (see text).

to *Zosterophyllum* or, as in Figure 12, it is sister to the clade giving rise to the zosterophyll-lycopsid groups. As a result it is part of the polychotomy of zosterophylls and lycopsids as shown in the consensus tree (Fig. 13). This differs from its present taxonomic placement in the rhyniophytes, indicating either that there is something significant about its relationships or that this placement is the result of incomplete knowledge of *Renalia*'s anatomy (xylem maturation unknown) and/or its very simple features.

The hypothesized relationships of zosterophylls to each other and to lycopsids are of interest in regard to Niklas & Banks's (1990) hypothesis concerning the existence of two major groups of zosterophylls, with lycopsids arising from the nonterminate group (= *Sawdonia* clade of this analysis). The presence of emergences, a linear sporangial

arrangement, circinate axes, and type of metaxylem wall pattern define the *Sawdonia* clade. In many of the most parsimonious trees, the *Sawdonia* (Niklas & Banks's nonterminate group) and *Asteroxylon* clades are sister to one another; six character state changes separate the *Sawdonia* clade from the *Asteroxylon* clade (includes lycopsids). These include character state changes in emergence presence/absence and type, metaxylem wall patterning, sporangial arrangement, tubercle presence and type, and circinate apices.

Hierarchical nesting of pre-lycopsids and lycopsids occurs in the *Asteroxylon* clade to the following extent. *Asteroxylon* is sister to the line including the remainder of taxa; at the next higher level, *Drepanophycus* is sister to the remainder. *Baragwanathia* is a sister taxon to a line including *Leclercqia*, *Lepidophloios*, and *Lycopodium*. Since
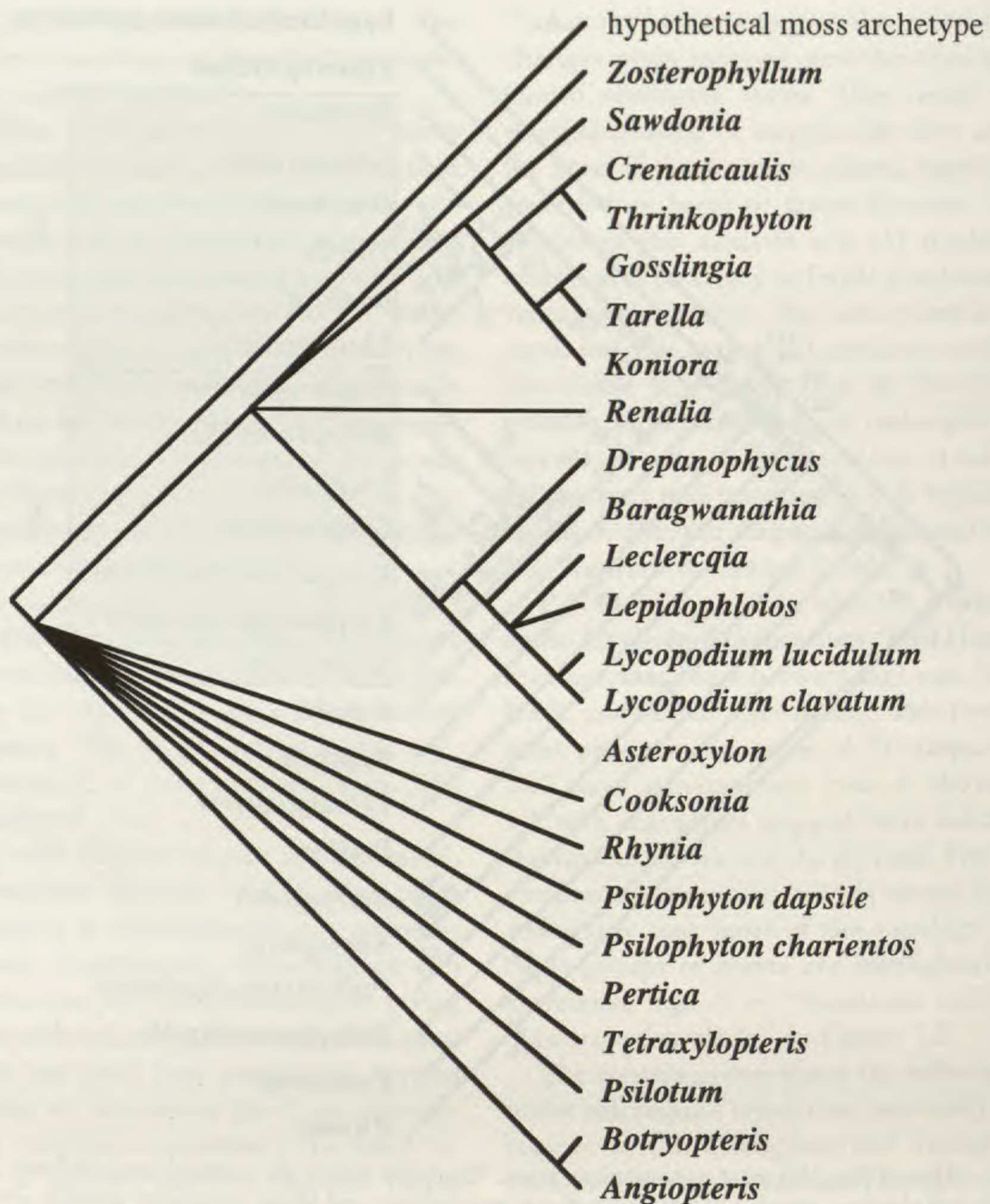
hypothetical moss archetype
Zosterophyllum
Sawdonia
Crenaticaulis
Thrinkophyton
Gosslingia
Tarella
Koniora
Renalia
Drepanophycus
Baragwanathia
Leclercqia
Lepidophloios
Lycopodium lucidulum
Lycopodium clavatum
Asteroxylon
Cooksonia
Rhynia
Psilophyton dapsile
Psilophyton charientos
Pertica
Tetraxylopteris
Psilotum
Botryopteris
Angiopteris

FIGURE 13. Combinable component consensus tree based on 350 most parsimonious trees. This differs only slightly from the strict consensus tree.

all are part of one clade, two alternative approaches can still be supported, namely, (1) abandon the Drepanophycales of Rayner (1984) and/or the "pre-lycopsid" concept and treat all as lycopsids in a broad sense, or (2) retain these groups as a means of recognizing some of the possible variation evident within this group (as is done throughout this paper). Better means are needed for resolving terminal taxa within the *Sawdonia* and *Asteroxylon* clades as well as within the polychotomy at the base of the cladogram.

On the consensus tree, the rhyniophytes, trimerophytes, ferns, and *Tetraxylopteris* form part of the large basal polychotomy. Again, survey of the most parsimonious trees shows that some relationships appear frequently; although details differ, the fern clade usually is most closely related to the *Psilophyton charientos* line, and *Tetraxylopteris*

is more closely related to *Pertica. Cooksonia, Rhynia,* and *Psilophyton dapsile* often are more closely related to one another than to other lineages. One manifestation of these relationships is shown in Figure 12.

The lack of resolution in the more basal regions of the trees reflects at least in part the conservative coding of certain characters and the low number of characters used. Some of the postulated relationships, and lack of resolution, of the trimerophytes, *Tetraxylopteris*, and the ferns may result from inclusion of grade-level taxa. Clearly, more information is needed about the earliest representatives of several plant lineages, about transformation possibilities of some characters, and about homology of structures. Also, early land plant lineages exhibit considerable homoplasy.

The cladograms shown in Figures 12 and 13

differ mostly in details from that illustrated by Crane & Hill (1987) for some early land plants. Their cladogram shows a zosterophyll–lycopsid line and a rhyniophyte–trimerophyte–progymnosperm line. Their method of analysis differs, fewer taxa were included, and some different characters were used. The trees illustrated here agree in suggesting a fairly close relationship between *Renalia* and the zosterophyll–lycopsid group, but differ in showing less resolution of rhyniophytes, trimerophytes, and progymnosperms.

The results, while preliminary, are interesting and disappointing. They represent an assessment of relationships obtained by an alternative means to the more traditional comparative discussion in the preceding sections (even though determining transformation series of some characters includes some traditional assumptions). However, some nodes are not very robust and homoplasies exist, so it is likely that different topologies will result when new data are obtained, and character assessment and determination of homologies are refined. Better topology exists at higher hierarchical levels in the cladogram, and some of this supports relationships as predicted from other forms of analysis. I regard this analysis as particularly valuable in suggesting that the morphology of these plants is not complex enough to assess affinities easily, since character definition and determination of homology is difficult. It points out areas where more information is needed. It also supports a closer relationship between lycopsids and zosterophylls than between lycopsids and any other lineage (except perhaps the *Renalia* lineage which, as mentioned previously, may be problematical), and in fact, the two lineages are monophyletic.

SUMMARY

In conclusion, zosterophylls constitute a fairly large and well-circumscribed group of early land plants, separate from trimerophytes or rhyniophytes. They exhibit many morphologic features similar to lycopsids, or ones that could easily be modified to result in a lycopsid. They appear similar in ecological tolerances. The existing cladograms support a monophyletic relationship between zosterophylls and lycopsids.

Areas in need of resolution (not only between zosterophylls and lycopsids, but with regard to all major lines of early land plants) include analysis of: (1) all types of conducting cells, steles, and stelar maturation and their homology; (2) homology among leaves; (3) how leaf-borne sporangia arose; and (4) the extent to which homoplasies occur

within the many types of early land plants that existed in the Silurian and Devonian. The time of appearance of major groups requires clarification. Definition of rhyniophytoids or cooksonioids and their putative relationship to tracheophytes is needed. Additional developmental data on extant (and extinct) lycopsids would aid in addressing questions of sporangium/sporophyll ontogeny and therefore better determine the relationship of sporangia to leaves versus stems in *Baragwanathia* and possibly some other taxa. Thus, the cladograms presented here help define the remaining problems, particularly the lack of definitive characters in several early land plant lineages that would allow better resolution of putative genealogies.

LITERATURE CITED

BANKS, H. P. 1968. The early history of land plants. Pp. 73–107 *in* E. T. Drake (editor), Evolution and Environment. Yale Univ. Press, New Haven.

———. 1975. Palaeogeographic implications of some Siluro–Early Devonian floras. Pp. 75–79 *in* K. W. S. Campbell (editor), Gondwana Geology. Australian National Univ. Press, Canberra.

——— & M. R. DAVIS. 1969. *Crenaticaulis*, a new genus of Devonian plants allied to *Zosterophyllum*, and its bearing on the classification of early land plants. Amer. J. Bot. 56: 436–449.

———, J. D. GRIERSON & P. M. BONAMO. 1985. The flora of the Catskill Delta clastic wedge. Special Pap. Geol. Soc. Amer. 201: 125–141.

BILDERBACK, D. E. 1987. Association of mucilage with the ligule of several species of *Selaginella*. Amer. J. Bot. 74: 1116–1121.

BONAMO, P. A. & J. D. GRIERSON. 1981. Leaf variation in *Leclercqia complexa* and its possible significance. Amer. J. Bot. Misc. Series Publ. 160: 42.

———, H. P. BANKS & J. D. GRIERSON. 1988. *Leclercqia, Haskinsia*, and the role of leaves in delineation of Devonian lycopod genera. Bot. Gaz. (Crawfordsville) 149: 222–239.

BOWER, F. O. 1935. Primitive Land Plants. Macmillan, London.

BRUCE, J. 1976. Development and distribution of mucilage canals in *Lycopodium*. Amer. J. Bot. 63: 481–491.

CHALONER, W. G. & P. MACDONALD. 1980. Plants invade the land. H. M. Stationery Office, The Royal Scottish Museum, Edinburgh.

——— & A. SHEERIN. 1979. Devonian macrofloras. *In*: House et al. (editors), The Devonian System. Special Papers in Palaeontology 23: 145–161.

CRANE, P. R. & C. R. HILL. 1987. Cladistic and paleobotanical approaches to plant phylogeny. Pp. 139–154 *in* H. M. Hoenigswald & L. F. Wiener (editors), Biological Metaphor and Cladistic Classification. Univ. of Pennsylvania Press, Philadelphia.

DONOGHUE, M. J., J. A. DOYLE, J. GAUTHIER, A. KLUGE & T. ROWE. 1989. The importance of fossils in phylogeny reconstruction. Annual Rev. Ecol. Syst. 20: 431–460.

DOYLE, J. A. & M. J. DONOGHUE. 1987. The importance

of fossils in elucidating seed plant phylogeny and macroevolution. Rev. Palaeobot. Palynol. 50: 63–95.

EAMES, A. J. 1936. Morphology of Vascular Plants. McGraw-Hill Book Co., New York.

EDWARDS, D. 1969. Further observations on *Zosterophyllum llanoveranum* from the Lower Devonian of South Wales. Amer. J. Bot. 56: 201–210.

———. 1970. Further observations on the Lower Devonian plant *Gosslingia breconensis* Heard. Philos. Trans., Ser. B. 258: 225–243.

———. 1975. Some observations on the fertile parts of *Zosterophyllum myretonianum* Penhallow from the Lower Old Red Sandstone of Scotland. Trans. Roy. Soc. Edinb. 69: 251–265.

———. 1976. The systematic position of *Hicklingia edwardii* Kidston & Lang. New Phytol. 76: 173–181.

——— & D. S. EDWARDS. 1986. A reconsideration of the Rhyniophytina Banks. *In:* R. A. Spicer & B. A. Thomas (editors), Systematic and Taxonomic Approaches in Palaeobotany. The Systematics Association Special Volume No. 31: 199–220. The Clarendon Press, Oxford.

——— & U. FANNING. 1985. Evolution and environment in the late Silurian–early Devonian: the rise of the pteridophytes. Philos. Trans., Ser. B 309: 147–165.

——— & P. KENRICK. 1986. A new zosterophyll from the Lower Devonian of Wales. J. Linn. Soc. Bot. 92: 269–283.

———, D. S. EDWARDS & R. RAYNOR. 1982. The cuticle of early vascular plants, and its evolutionary significance. Pp. 341–361 *in* D. F. Cutler et al. (editors), The Plant Cuticle. Linn. Soc. Sympos. Ser. 10. Academic Press, New York.

———, P. KENRICK & L. M. CARLUCCIO. 1989. A reconsideration of cf. *Psilophyton princeps* (Croft & Lang, 1942), a zosterophyll widespread in the Lower Old Red Sandstone of South Wales. J. Linn. Soc., Bot. 100: 293–318.

EDWARDS, W. N. 1924. On the cuticular structure of the Devonian plant *Psilophyton*. J. Linn. Soc., Bot. 46: 377–385.

EL-SAADAWY, W. & W. S. LACEY. 1979. Observations on *Nothia aphylla* Lyon ex Hoeg. Rev. Palaeobot. Palynol. 27: 119–147.

ESAU, K. 1965. Plant Anatomy, 2nd edition. John Wiley & Sons, New York.

FAIRON, M. 1967. L'*Asteroxylon elberfeldense* Kräusel and Weyland porte-t-il des axes terminaux du type *Hostimella hostimensis* Potonié et Bernard? Extr. Ann. Geol. Soc. Belg. X: 7–30.

FAIRON-DEMARET, M. & H. P. BANKS. 1978. Leaves of *Archaeosigillaria vanuxemii*, a Devonian lycopod from New York. Amer. J. Bot. 65: 246–249.

GENG, B-Y. 1985. *Huia recurvata*, a new plant from Lower Devonian of southeastern Yunnan, China. Acta Bot. Sin. 27: 419–426.

GENSEL, P. G. 1976. *Renalia hueberi*, a new plant from the Lower Devonian of Gaspé. Rev. Palaeobot. Palynol. 22: 19–37.

———. 1982a. A new species of *Zosterophyllum* from the early Devonian of New Brunswick. Amer. J. Bot. 69: 651–669.

———. 1982b. *Oricilla*, a new genus referable to the zosterophyllophytes from the late Early Devonian of New Brunswick. Rev. Palaeobot. Palynol. 37: 345–359.

———. 1991. Notes on the cuticular morphology of *Sawdonia acanthotheca*, particularly in regard to emergences. Neues Jahrbuch für Geologie und Paläontologie, Abhandlunger 183: 49–59.

——— & H. N. ANDREWS. 1984. Plant Life in the Devonian. Praeger, New York.

———, ——— & W. H. FORBES. 1975. A new species of *Sawdonia* with notes on the origin of microphylls and lateral sporangia. Bot. Gaz. 136: 50–62.

———, A. E. KASPER & H. N. ANDREWS. 1969. *Kaulangiophyton*, a new genus of plants from the Devonian of Maine. Bull. Torrey Bot. Club 96: 265–276.

GERRIENNE, P. 1988. Early Devonian plant remains from Marchin (North of Dinant Synclinorium, Belgium), I. *Zosterophyllum deciduum* sp. nov. Rev. Palaeobot. Palynol. 55: 317–335.

HAO, S.-G. 1988. A new Lower Devonian genus from Yunnan, with notes on the origin of leaf. Acta Bot. Sin. 30: 441–448.

———. 1989. A new zosterophyll from the Lower Devonian (Siegenian) of Yunnan, China. Rev. Palaeobot. Palynol. 57: 155–171.

HEARD, A. 1927. Old Red Sandstone plants showing structure, from Brecon (South Wales). Quart. J. Geol. Soc. London. 83: 195–209.

HÉBANT, C. 1977. The conducting tissues of bryophytes. *Bryophytonianum Bibliotheca* 10. J. Cramer, Vaduz.

HUEBER, F. M. 1970. *Rebuchia*: a new name for *Bucheria* Dorf. Taxon 19: 822.

———. 1971a. *Sawdonia ornata*: a new name for *Psilophyton princeps* var. *ornatum*. Taxon 20: 641–642.

———. 1971b. Early Devonian plants from Bathurst Island, District of Franklin. Geol. Surv. Canada. Pap. 71–28: 1–17.

———. 1972. *Rebuchia ovata*, its vegetative morphology & classification within the Zosterophyllophytina. Rev. Palaeobot. Palynol. 14: 113–127.

———. 1982. *Taeniocrada dubia* Kr. & W.: its conducting strand of helically strengthened tubes. Bot. Soc. Amer. Misc. Series Pub. No. 162: 58–59.

——— & H. P. BANKS. 1979. *Serrulacaulis furcatus*, gen. et sp. nov., a new zosterophyll from the lower Upper Devonian of New York State. Rev. Palaeobot. Palynol. 28: 169–189.

KENRICK, P. & P. R. CRANE. 1991. Water-conducting cells in early fossil land plants: implications for the early evolution of tracheophytes. Bot. Gaz. 152: 335–356.

——— & D. EDWARDS. 1988a. The anatomy of Lower Devonian *Gosslingia breconensis* Heard based on pyritized axes, with some comments on the permineralization process. J. Linn. Soc., Bot. 97: 95–123.

——— & ———. 1988b. A new zosterophyll from a recently discovered exposure of the Lower Devonian Senni Beds in Dyfed, Wales. J. Linn. Soc., Bot. 98: 97–115.

LANG, W. H. & I. C. COOKSON. 1935. On a flora, including vascular land plants, associated with *Monograptus*, in rocks of Silurian age, from Victoria, Australia. Philos. Trans., Ser. B. 224: 421–449.

LELE, K. M. & J. WALTON. 1961. Contributions to the

Volume 79, Number 3
1992

Gensel
Phylogenetic Relationships of the
Zosterophylls and Lycopsids

473

knowledge of "Zosterophyllum myretonianum" Penhallow from the Lower Old Red Sandstone of Angus. Trans. Roy. Soc. Edinburgh 64: 469–475.

LI, C.-S. 1982. *Hsüa robusta*, a new land plant from the Lower Devonian of Yunnan, China. Acta Phytotax. Sin. 20: 331–342.

MISHLER, B. D. & S. P. CHURCHILL. 1985. Transition to a land flora: Phylogenetic relationships of the green algae and bryophytes. Cladistics 1: 305–328.

MUSTAFA, H. 1978. Beiträge zur Devonflora III. Argumenta Palaeobotanica 5: 91–132.

NIKLAS, K. J. 1984. Size-related changes in the primary xylem anatomy of some early tracheophytes. Paleobiology 10: 487–506.

———. 1985. The evolution of tracheid diameter in early vascular plants and its implications on the hydraulic conductance of the primary xylem strand. Evolution 39: 1110–1122.

——— & H. P. BANKS. 1990. A reevaluation of the zosterophyllophytina with comments on the origin of lycopods. Amer. J. Bot. 77: 274–283.

PENHALLOW, D. P. 1892. Additional roles on Devonian plants from Scotland. Canad. Rec. Sci. 5: 1–13.

RAYNER, R. J. 1983. New observations on *Sawdonia ornata* from Scotland. Trans. Roy. Soc. Edinburgh, Earth Sciences 74: 79–93.

———. 1984. New finds of *Drepanophycus spinaeformis* Göppert from the Lower Devonian of Scotland. Trans. Roy. Soc. Edinburgh, Earth Sciences 75: 353–363.

REMY, W., S. SCHULTKA & H. HASS. 1986. *Anisophyton gothani* nov. gen., nov. spec. und hinweise zur stratigraphie der südlichen Wilbringhauser Scholle. Argumenta Palaeobotanica 7: 79–107.

SATTLER, R. 1988. Homeosis in plants. Amer. J. Bot. 75: 1606–1617.

——— & U. MAIER. 1977. Development of the epiphyllous appendages of *Begonia hispida* var. *cu-*

cullifera: implications for comparative morphology. Canad. J. Bot. 55: 411–425.

SCHOCH, R. 1986. Phylogeny Reconstruction in Paleontology. Van Nostrand Reinhold, New York.

SCHWEITZER, H. J. 1979. Die Zosterophyllaceae des rheinischen Unterdevons. Bonner Palaeobot. Mitt. no. 3.

———. 1980. Uber *Drepanophycus spinaeformis* Göppert. Bonner Palaeobot. Mitt. no. 7.

———. 1983. Die Unterdevonflora des Rheinlandes I. Palaeontographica 189B: 1–138.

SHUTE, C. H. & D. EDWARDS. 1989. A new rhyniopsid with novel sporangium organization from the Lower Devonian of South Wales. J. Linn. Soc., Bot. 100: 111–137.

STEIN, W. E. 1987. Phylogenetic analysis and fossil plants. Rev. Palaeobot. Palynol. 50: 31–61.

——— & C. B. BECK. 1987. Paraphyletic groups in phylogenetic analysis: Progymnospermopsida and Préphanérogames in alternative views of seed plant relationships. Bull. Soc. Bot. France 134: 107–119.

STEWART, W. N. 1983. Paleobotany and the Evolution of Plants. Cambridge Univ. Press, London.

SYKES, M. G. 1908. Notes on the morphology of the sporangium-bearing organs of the Lycopodiaceae. New Phytol. 7: 41–60.

TAYLOR, T. L. 1988. The origin of land plants: some answers, more questions. Taxon 37: 805–833.

TIMS, J. D. & T. C. CHAMBERS. 1984. Rhyniophytina and Trimerophytina from the early land flora of Victoria, Australia. Palaeontology 27: 265–279.

ZAKHAROVA, T. V. 1981. On the systematic position of the species '*Psilophyton goldschmidtii*' from the Lower Devonian of Eurasia. Paleontol. Žurn. 23: 111–118.

ZDEBSKA, D. 1982. A new zosterophyll from the Lower Devonian of Poland. Palaeontology 25: 247–263.

THOUGHTS ON THE EARLY LYCOPSIDS AND ZOSTEROPHYLLS[1]

Francis M. Hueber[2]

ABSTRACT

Morphological, anatomical, and reproductive characteristics of the modern lycopsids are of great value in tracing the ancient lineage of the group. The sporangium is the principal character: lack or misinterpretation of it in fossil specimens places an investigator in a predicament. An informed choice of a group of characters must be made from all those that remain. There are, of course, pitfalls and the defining characters of fossil species of the lycopsids have become confused. Differences in ontogeny of sporangia in early land plants are suggested as a way of separating the early rhyniophytoids with terminal, fusiform, indehiscent sporangia from the cooksonioid plants with terminal, globular or reniform, dehiscent sporangia. The rhyniophytoids are the source of later plant groups other than the lycopsids. Among the cooksonioids, change in the ontogeny of the sporangium in relation to the apical meristem is suggested as the point of differentiation and separation of the zosterophyll and lycopsid lineages. A reinterpretation of *Kaulangiophyton* suggests that its sporangia are borne adaxially on the leaves rather than terminally on stalks. The apical meristem of *Asteroxylon* is illustrated and described for the first time and compared with the apical meristem seen in species of *Lycopodium*. The genus *Baragwanathia*, questionably the earliest in the lycopsid lineage, is discussed in light of specimens ostensibly dated as of Gorstian age (lower Late Silurian) in Australia. *Drepanophycus* is perhaps the earliest recognizable member of the lycopsid lineage as opposed to *Baragwanathia*. The variation in the morphology of lycopsid leaves is of taxonomic value only in differentiating genera, particularly among those in the Devonian. Lineages are suggested diagrammatically.

The adage that the present is the key to the past is one of the basic principles in paleobotanical research. Careful study of the anatomy, morphology, modes of reproduction, and habitats of the components of our modern floras is the basis for extrapolation of such study into the framework of the fossil record. Unfortunately, deficiencies in the fossil record are often barriers to orderly reconstruction of floras at many taxonomic and nomenclatural levels. We are fortunate that the ancient lineage of the lycopsids is reasonably well preserved so that reconstruction of the variations within the group through time can be made with some degree of confidence. The presence of members of the lineage in our modern floras further eases the task.

CHARACTERIZATION OF MODERN LYCOPSIDS

What is the group of characteristics used to define modern lycopsids? How many of the identifying characteristics persist or are sufficiently well preserved to identify a particular fossil with confidence as a lycopsid? The following is a summary of key characters that can be gleaned from general botany texts, taxonomic monographs, or texts on plant morphology and anatomy. The presence or absence of individual characteristics may be recorded directly from observation and preparation of a particular fossil plant or interpreted from the mode and matrix in which the plant was originally entombed. The characteristics of lycopsids are:

Vascular plants with stems, roots (not rhizoids), and leaves, reproduction vegetative and by spores; terrestrial or epiphytic; *Stems* recumbent, ascending, clambering, or twining; branching dichotomous to pseudomonopodial; herbaceous, arboreous, or arborescent (fossil record only); *Roots* adventitious, from stem (*Lycopodium*), or rhizophore (*Selaginella*); from root meristem in rhizomorph (*Isoetes*); branching dichotomously, usually monarch; *Leaves*

microphyllous, entire, serrate, or dentate; simple, or divided (fossil record); arranged in helices, alternately, decussately, or randomly; *Eusporangiate sporangium*, borne on adaxial surface of normal leaf, or modified leaf; sessile on leaf surface; in axil of a leaf; on a "short stalk" on the stem, just above a leaf; in strobili, or in alternating fertile and sterile regions on the stem; dehiscence by a slit, distally, transversely to leaf, or distally, longitudinally to leaf, or low, outer side (distally on leaf), or low, inner side (proximally on leaf); *Vascular strand* protostelic, or siphonostelic; maturation exarch, or mesarch; terete, variously lobed, or variously dissected; traces to leaves extend upwardly from the ridges of the xylem entering the leaf as a single vein. Of all the characteristics listed here, the only one that consistently unites the Lycopsida as a group is the eusporangiate ontogeny of the sporangium and its position in relation to the microphyllous leaf. The remaining characteristics serve in the definition of the orders, families, genera and species within the class. All of these details are easily obtained from specimens of the Recent Lycopsida. However, in the study of fossilized plant remains, the absence of the principal character of the sporangium places the investigator in a predicament wherein a group of characters must be chosen from among all of those that remain. The choices, interpretations, and conclusions may not be satisfactory, and the concept of the fossil elements of the Lycopsida may become confused. As examples of a few of the pitfalls in interpreting the true morphology of leaves in the early lycopsids, Figure 1A–C illustrates three specimens of *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland, 1948. The leaves as seen in lateral view in Figure 1A appear to be upwardly turned and spinelike, but in another specimen from the same horizon (Fig. 1B) the leaves appear flattened and laminate. The third specimen (Fig. 1C), from a nearby horizon, represents a partially permineralized axis in which the leaves are seen in transverse section as having a slightly flattened adaxial surface and a more rounded abaxial surface. If there were only one specimen available, the description of the leaf morphology would be unrepresentative. Occasionally a specimen will exhibit two differing morphologies of the leaves due to the mode of preservation. In Figure 1D, an unidentified lycopsid, the axis is slightly twisted and buried in the matrix in three-dimensional form such that the leaves appear spinelike in lateral view due to vertical compression, but rounded in cross section where they are not compressed. Figure 2C illustrates an axis on which the leaves appear long

and acicular on the right side of the specimen but appear trifurcate along the left side. Such leaves are characteristic of *Colpodexylon* Banks, 1944 as illustrated here in Figure 2D. The morphology of the leaves alone does not identify the fossils as lycopsids, but the arrangement of the leaves in helices on axes exhibiting other characteristics attributable to the group make the identifications more credible. Axes of the type illustrated in Figure 2E, in which the vascularized spinelike appendages are widely spaced and seem not to be in any specialized arrangement, beg for classification and lack any tenable lycopsid characteristics.

Morphology of the leaves in the fossil lycopsids is of taxonomic value, but the morphology of decorticated axes among the early lycopsids, as discussed extensively by Grierson & Banks (1963) and Bonamo et al. (1988), in most instances precludes the positive identification of genera. I will not discuss the subject further here, but I will illustrate one of the peculiarities of compressed, decorticated axes of fossil lycopsids. In Figure 2A and 2B, the interpretation of the images of the fossil is directly influenced by the angle and direction of the light source used in producing the photographs. Both Figure 2A and 2B can be inverted and the effect thereby reversed. Are there "leaf bases" elevated on the surface of the specimen, or are there depressions that reflect the gaps in the hypodermis through which the vascular trace and adjunct tissues passed into the leaf? One cannot become too confident in the identification of the early lycopsids, but when the fossil material exhibits sufficient intrinsic detail and when additional details can be interpreted from the matrix and occurrence, an identification can be reached with considerable confidence.

SPORANGIA: MORPHOLOGY AND POSITION IN EARLY LAND PLANTS

Among the vascular plants in the Silurian–Early Devonian, the vegetative axes are similar in basic architecture; however, the morphologies of the sporangia are very different. All of the genera have small, naked axes, with the exception of *Baragwanathia* Lang & Cookson, 1935, which has large, leafy axes. The sporangia may be (1) fusiform or obovate, indehiscent, and borne terminally on the axes; (2) reniform, distally dehiscent, and borne terminally on primary axes; (3) reniform, distally dehiscent, and borne terminally on secondary, lateral shoots; or (4) reniform, distally dehiscent, and borne in the axil or on the adaxial surface of a leaf or on the stem immediately above a leaf. *Stegano-*